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ECOLOGY.—*Progress in utilization standards for western ranges.*[1] R. S. CAMPBELL, U. S. Forest Service. (Communicated by W. R. CHAPLINE.)

Range utilization is essential to the welfare of the West and of the United States as a whole. The western range territory provides one-third of the cattle and calves, two-thirds of the sheep, and three-fourths of the wool and mohair grown in the United States. These livestock products are important even in ordinary times. They are indispensable during war. Because of the huge armed force, millions of war workers at strenuous toil, and lend-lease aid to the Allies, the country each year is using double its domestic wool production, and civilian meat consumption has been cut by more than one-third in order to balance consumption with supply.

Within the western range territory the animals producing these requisite supplies graze part or all of the year on range forage —on the grasses, other herbs, and shrubs growing in a generally rather thin stand on land best suited to use by domestic livestock. The area devoted to this use is about 728,000,000 acres, nearly two-fifths of the entire United States. The harvesting of the edible portions of this plant growth each year requires careful management to prevent excessive damage to the range resource and to permit sustained production of forage and livestock.

Range management is the regulation, direction, and control of grazing with the object of the fullest possible use of the forage resource consistent with other range land uses. Man's main control is over the livestock; hence the four principal features of range management are: the most appropriate kind of animals, correct seasonal use, even distribution of grazing, and proper numbers of livestock. The other three features of management are most effective only when numbers of livestock are correct —thus indicating the importance of proper utilization of the range forage each year.

Utilization standards is a term employed to designate a wide variety of information needed by the range manager in understanding and currently judging the utilization and the relative condition or productivity of the range. Utilization is a complex problem, dealing with hundreds of valuable forage plants of several life forms growing on ranges from the high rainfall mountain lands down to low value semidesert shrub areas. Involved are several stages of plant succession, considerable differences between species as to the relish with which they are eaten by livestock at different seasons, resistance to grazing and processes of growth, maintenance, and reproduction. In fact, the whole field of range plant and animal ecology is involved. The job in range utilization standards is to work out answers to some of the more pressing problems of forage utilization by livestock, to take advantage of findings from other pertinent studies, and to formulate the essential results into simple, readily applicable facts for use by busy range administrators and managers. The purpose of this paper is to describe some of the recent advances in this field.

A considerable body of range management information, much of it relating to utilization, has been accumulated during

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the past few decades. The U. S. Department of Agriculture has been interested in range problems since its establishment in 1862, and early-day studies of forage plants, reseeding, and grazing brought together helpful facts on the nature and extent of the resource. National-forest range-management studies, begun in 1907 by James T. Jardine (1910) and A. W. Sampson (1909), in cooperation with F. V. Coville, of the Bureau of Plant Industry, gradually brought together biological facts on the grazing habits and forage requirements of range sheep and cattle, and the growth and use of range forage. These early studies, including both the range vegetation and livestock grazing, led quickly into practical management features such as the bedding out system of handling sheep, water development, correct seasonal grazing, deferred and rotation grazing, and forage inventory through range surveys.

Increasing attention was given the problem of forage utilization until in 1936 a special project was started, primarily to develop improved utilization standards for application on the 87,000,000 acres of national-forest range (Campbell, 1937). It was undertaken by the Division of Range Research and the six western forest and range experiment stations and administrative regions. The immediate job was to evaluate all pertinent data and formulate the best possible standards, mainly in handbook form, for immediate use. At the same time the whole utilization problem was carefully analyzed for the most urgent questions. By 1939, the project turned toward research primarily ecological. The work aimed at these important problems was seriously restricted by limited funds. This work was only in its initial stages when wartime demands for livestock products dictated an immediate program to furnish the best available standards to help both public and private agencies attain maximum sustained production.

The subject of utilization standards can best be presented under two broad headings: (1) range condition, including changes and trends in condition; and (2) range utilization, including methods of measurement and the determination of proper utilization.

RANGE CONDITION

Range condition is the relative state of health or productivity of the range, including both the soil and the forage, in relation to its potential state and the best practicable management. The inclusion of information on range condition in utilization standards requires answers to such basic questions as the following:

1. What are the main range types for which utilization standards are needed?

2. What should be the objective toward which management of each type should aim (in terms of plant cover and soil condition)?

3. What annual or seasonal variations are there in habitat and plant cover that can be recognized in the field?

The answers to these questions draw on practically all phases of range ecology, from vegetation surveys to studies of plant competition and succession. Broad vegetation types include the tall grass, shortgrass, Pacific bunchgrass, semidesert grass, sagebrush, etc., within which are important subtypes requiring individual consideration. Thus, within the open forest type are such important subtypes as the ponderosa pine bunchgrass, the alpine grassland, aspen-fir, mountain brush, and others.

The early studies of Sampson (1919) on plant succession in relation to range management furnished a working method of setting up the objective toward which management should aim on a specific type. He identified four vegetation types or stages that feature plant succession from a depleted condition on subalpine grasslands in central Utah; (1) early-maturing annuals growing on gravelly loam poor in organic matter and moisture; (2) perennial herbs, on soil containing moderate amounts of organic matter and moisture; (3) aggressive perennial grasses with herbs and shrubs on soil with still better organic and moisture content; and (4) deep-rooted or densely tufted perennial grasses on fine soil high in organic matter and available moisture. Sampson determined that overgrazing caused retrogression by destroying the ground cover and allowing loss of soil fertility. He also found that grassland in climax condition furnishes abundant forage, withstands grazing better, and has more

stable soil than when it is in the lower developmental stages.

More recently Pickford and Reid (1942), working on subalpine grasslands in northeastern Oregon, identified stages similar to those of Sampson. They found that the climax stage is characterized by stable, fertile soil, ample desirable forage, and uniform, silt-free streamflow. Green fescue (*Festuca viridula*) is dominant, covering at least half the ground surface.

Subalpine ranges in the mixed grass and weed stage are in only fair condition, since they produce less than the maximum amount of forage and their watershed values are impaired. They have an open stand of vegetation that rarely covers more than one-third of the ground surface. Subclimax grasses are abundant and compete successfully with better forage species for available soil moisture. Weeds are common and accelerated erosion is conspicuous on exposed soil surfaces and pedestaled fescue tussocks.

A still poorer condition is represented by the second weed stage, in which the stand of vegetation is very open and green fescue is represented only by scant remnant plants. Low value weeds and shrubs are abundant, and the soil is clearly eroded, with deep gullies on hillsides and cut channels.

The importance of maintaining ranges in good condition is shown by the grazing capacity of the various stages. Grazing capacity of the near climax green fescue stage, having good soil condition, was more than four times that of ranges in the poor condition represented by lower stages.

Similar stages and corresponding grazing values have been worked out in greater or less detail for several other important types or subtypes throughout the West.

TREND OF RANGE CONDITION

The range manager must know whether his management is bettering the condition and increasing the forage production of his range, or causing it to go on the downgrade. Range trend is the direction and amount of change in range condition. Much of the range land of the West is in some stage of depletion, varying from slight to very severe. The problem of first importance on these deteriorated ranges is to stop the retrogression and start the process of improvement. With the widely varying degree of deterioration of vegetation and soil on different ranges, the determination of range trend is not simple. Improvement or deterioration can be recognized from such features as the vigor of the principal forage species, the species reproducing and becoming established, and character of soil erosion. But it requires extraordinary alertness and ingenuity in the field of dynamic ecology to detect incipient changes and particularly to interpret the natural changes due to variable weather, and to evaluate such changes along with those caused by livestock grazing. For example, broom snakeweed (*Gutierrezia sarothrae*) is a low-growing aggressive shrub with little or no forage value. It has been shown that the occurrence of a dense stand of young thrifty snakeweed plants on range where the palatable black grama (*Bouteloua eriopoda*) has been weakened by overgrazing, represents a definite downward trend (Campbell and Bomberger, 1934). Both the snakeweed and the black grama may be injured by drought, but through careful utilization of the valuable grass, deterioration can be stopped, and at this stage recovery need not be difficult nor require more than a few years.

On the other hand, the invasion of a dense stand of snakeweed on a badly depleted, wind-blown, honey-mesquite (*Prosopis glandulosa*), sand-dune type represents a definite upward trend through stabilizing and building up the soil and affording protection for better forage plants ultimately to grow. Ranges that have reached this low ebb of productivity require many decades to restore a grass stand of reasonably good productivity. However, the occurrence of dense stands of such low value plants as snakeweed is not the final criterion of range condition—it is only one of many important features that must be interpreted in the aggregate.

Advanced deterioration is rather easily recognized by the thin stand of perennial grasses and obviously accelerated erosion, but the early symptoms of deterioration are more difficult to detect. Some of the more

striking signs of a deteriorating range developed to date include: (1) weakened vitality of the important forage plants, as shown by sickly color and reduced height and volume; (2) thinning of the perennial grass cover as indicated by accelerated dying out and disintegrating of tufts; (3) replacement of good forage plants with poor ones, as indicated by abundance of young inferior plants; and (4) accelerating erosion, as evidenced by soil washing on slopes, a distinct increase in number of recent small pencil or finger gullies, and failure of vegetation to grow in small gullies.

In general, an upward trend is indicated by:

1. Arresting of accelerated erosion, perennial vegetation established on eroded banks of drainage channels, no exposed grass roots, soil pedestals with sloping rather than vertical sides, and root crowns of perennial grasses not buried with silt, etc.

2. Vigorous appearance of the stand of forage plants.

3. Noticeable reproduction or spread of plants of the next higher succession stage.

4. Exposed mineral soil colonized with young plants of perennial species.

These and other indicators have been worked out more specifically for several types in the West, but a great deal more remains to be done, both on other types and on more accurate and reliable indicators of range trend.

FACTORS INFLUENCING UTILIZATION

A thorough knowledge of forage utilization is essential because livestock grazing is a major influence in causing the great differences in values between ranges in good and poor condition. Among the important factors influencing forage utilization are the kind and number of livestock; their eating habits; their forage preferences involving succulence, taste, and other qualities of the forage plants; the season of use, the plant composition, and the distribution of livestock over the range.

As to kind of livestock, cattle generally prefer grasses and shrubs, and horses choose grass, while sheep and goats prefer weeds and browse plants, although all animals like some variety in their diet. Soil disturbance through trampling also varies with the animals and particularly with their handling. Thus, poor herding of sheep in compact, fast-moving bands can cause serious overutilization and trampling, whereas open herding and gentle handling can utilize most ranges without serious damage.

Season of grazing is very important in securing utilization of plants when they are palatable. For example, in the Southwest tobosa grass (*Hilaria mutica*) is good forage during summer when it is green and succulent, but after that time it becomes so dry and woody that livestock do not graze it willingly. Correct season of grazing is also very important in allowing the main forage plants ample opportunity to grow and reproduce. Craddock and Forsling (1938) found in southern Idaho that the start of growth on sagebrush-grass ranges was far too variable to allow grazing to begin then. They found a minimum variation in the time when perennial grasses reached a 2-inch height growth and recommended beginning grazing at that stage of development so as to assure sufficient available forage for the livestock and to permit the forage growth to keep ahead of the sheep grazing.

The effect of a number of factors on utilization of black grama by cattle is brought out in a 7-year study on several thousand acres of the Jornada Experimental Range in southern New Mexico. By means of multiple regressions applied to nearly 750 measurements, it was found that percent height utilization of black grama varied significantly with intensity of pasture stocking and distance from livestock water (Fig. 1). The average effect of each additional mile from a livestock watering place was a decrease of 10 percent in utilization of black grama, out to a maximum distance studied of 3.5 miles. When black grama in a pasture was fully utilized on the average, it was overutilized out to 2 miles from water. Under moderate or conservative pasture grazing, the grama was grazed too closely only out to half a mile from water, and rather lightly beyond 3 miles. With light pasture use, the black grama was utilized very lightly at 2 miles from water and was

too closely grazed only in the first one-fourth mile from water.

The effect of distance from salt grounds on utilization of black grama was not great —averaging only 1.3 percent utilization per mile. But improved salting in a properly stocked individual pasture increased the utilization of black grama as much as 10 to 15 percent at 3 miles or more from water.

Other factors were also important. There was higher utilization of black grama near the main roads and well-traveled trails. Also black-grama utilization on the average increased 4 percent for each 0.1 decrease in

DETERMINING PROPER UTILIZATION

Research has employed a number of ways to get at proper utilization which is really the heart of utilization standards. The maintenance of black grama on meter quadrats on range grazed to different degrees was measured by Nelson (1934) on the Jornada Experimental Range. On ungrazed plots, there was a considerable change in tuft area, increasing or decreasing from one year to the next in response to the rainfall of the preceding summer. Further, the average density of black grama over a 13-year period under conservative or moderate

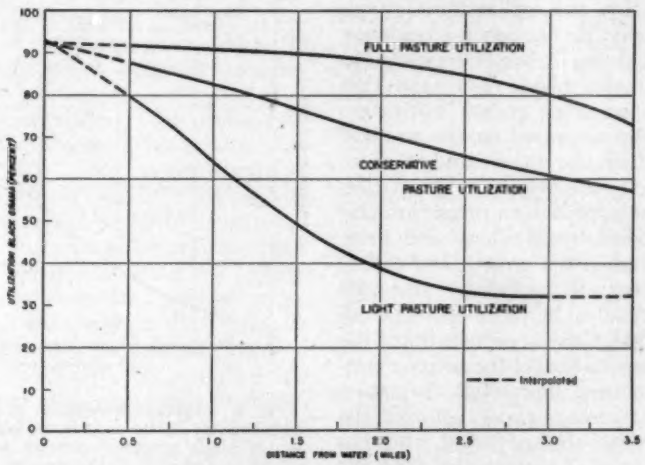

Fig. 1.—Average utilization of black grama by cattle in percent height at different distances from water under full, conservative or moderate, and light pasture utilization, Jornada Experimental Range, southern New Mexico, 1931 to 1937, inclusive.

black grama density after allowing for other factors. Thin stands or scattered plants of black grama were fully utilized out to 3 or 4 miles from water, with only moderate pasture stocking. This brings out the importance of protecting and managing the utilization of the important forage species on depleted types, if they are to be restored to their potential productivity.

Similar studies of important factors influencing utilization on pine bunchgrass range in northern Arizona by Glendening, and on mountain bunchgrass range in central Utah by Clark, are as yet unpublished.

grazing was little different from that under no grazing. Slight overuse of black grama in dry years prevented maximum development of the stand and permitted inferior associated grasses and weeds to secure a foothold on the depleted grama areas. Heavy overgrazing year after year practically killed out the black grama stand and caused very unstable soil conditions. Under moderate grazing, sufficient plant stubble and stolons remained each year to assure good growth and reproduction of the stand the next year.

Persistent clipping of all black grama herbage on plots to a 2-inch height or less

over a 10-year period was found by Canfield (1939) to result in greatly reduced yield and eventually destroyed or killed the plants. In similar studies on clipped tobosa-grass plots, cropping to 2 inches was too close, but clipping to 4 inches maintained a high forage yield and stimulated vegetative reproduction.

Clark, at the Intermountain Forest and Range Experiment Station, working with slender wheatgrass (*Agropyron trachycaulum*) and mountain brome (*Bromus carinatus*) on the Wasatch Plateau in central Utah, has marked individual plants grazed to different degrees and has followed the forage production and utilization through subsequent years. He has noted a tendency for the sheep to come back and graze closely the younger smaller plants each year. This suggests that on some ranges utilization may need to be measured on the younger plants rather than the entire stand, in order to perpetuate the important forage species.

Still another approach to proper utilization was followed by McCarty and Price (1942) who studied the growth and carbohydrate content of important perennial grasses and broadleaf herbs on central Utah mountain ranges. Critical periods in the life cycle were found to be: (1) the active reproductive period from flowerstalk formation through seed ripening, and (2) during the early carbohydrate storage period, when the plant is in a period of recuperation from the reproductive period. A system of rotation grazing in which portions of the range are grazed at a different time each year allows a periodic slackening in the intensity of grazing during these periods in the plants' life processes.

It is not a simple task to express these findings for practical application on the range. One common way is to describe the stubble height that should be left ungrazed for the important forage species. Studies both in the Northwest and in the Southwest show a considerable proportion of ungrazed plants on properly grazed range. Still another way of defining proper use is in percentage of herbage removal.

The difficulty with any statement of proper utilization, whether expressed in stubble height or in percentage removal, is that extreme care is needed in applying it to any area other than where it was developed. Weakened forage plants on deteriorated ranges can not resist the same degree of utilization as thrifty vigorous plants on ranges in good condition. Ordinarily the better forage plants should be grazed less on deteriorated range in order to hasten restoration. Also, they should be used less on steep slopes, particularly on more erosive soils.

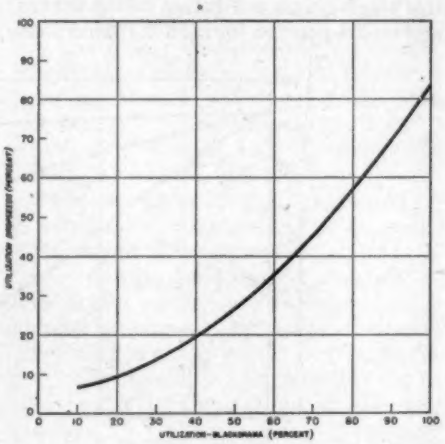

Fig. 2.—Average utilization of sand and mesa dropseeds by cattle at various degrees of utilization of black grama in percent height as determined at the end of the grazing year in June, Jornada Experimental Range, 1931 to 1937, inclusive.

In the final proper use rating, the key forage plants are assigned values mainly on their resistance to grazing, including ability to survive drought and normal competition, and with due allowance for other factors. Less important species are rated at the degree to which they are actually grazed when the key species are properly utilized. This is illustrated in the curve of utilization found between black grama and sand and mesa dropseeds (*Sporobolus cryptandrus* and *S. flexuosus*), less valuable species (Fig. 2). When the black grama was grazed at about 85 percent or proper on this scale, the dropseeds were grazed about 65 percent of their height.

All these results find direct application in the control of livestock grazing on the range. But intelligent control of numbers and distribution of animals on the range requires careful checks of actual forage utilization.

MEASURING RANGE UTILIZATION

Several methods of measuring range utilization have been developed, suited to various purposes and types of vegetation. The most common method now employed by range administrators is the so-called reconnaissance or ocular inspection system, in which the range is systematically examined and the utilization estimated directly, either in descriptive terms or preferably in percentage herbage removal. Frequent close examination of individual plants on small areas a few square feet in size is necessary for reasonable accuracy.

A more accurate way is the ocular estimate by plot method described by Pechanec and Pickford (1937), who tested a number of methods in southern Idaho. The examiner estimates percentage weight removal of herbage from forage species on a series of circular plots each containing 100 square feet. In training, ungrazed vegetation on plots is clipped and weighed, the utilization estimated, then the balance clipped and weighed as a check until the examiner can judge utilization with reasonable accuracy. This method has been found admirably suited for research purposes on grasses, weeds, and browse. Pickford, working in the Northwest, has recently tested the method as an administrative tool on national-forest ranges. Proposed standardized instructions for its application are being considered in the several Western Regions of the Forest Service.

Another method of determining utilization that has found widespread application is the use of grass height-weight or volume tables. The height of grazed stubble is expressed in percent and converted to percentage weight utilization by means of charts or scales showing height-weight relationships of the important forage species. This method is based on the assumption that most grasses have a reasonably constant distribution of weight throughout the plant in relation to height. Three distinct types, all with flower stalks, are indicated in the curves shown in Fig. 3. Bottlebrush squirreltail (*Sitanion hystrix*) has a nearly straight line relationship, with weight distributed about equally through the plant from the top of the tallest flower stalk. Blue grama (*Bouteloua gracilis*) has a gentle curve, with about 80 percent of the weight in the bottom half of the plant owing to the abundance of basal leaves. Sandberg bluegrass (*Poa secunda*) has a slight "S" curve because of heavy seed heads and high concentration of weight in the basal leaves. Curves for plants without seedstalks are still somewhat different. Application of these tables in the field requires great care, because Clark (1943) has found significant differences within the same species in different years and in different altitudinal zones in central Utah.

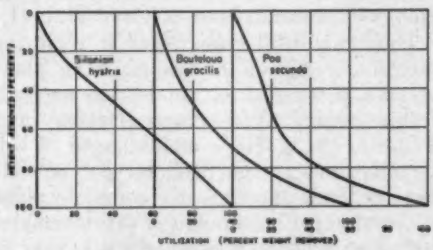

Fig. 3.—Three types of height-weight curves of range grasses, all with seedstalks: bottlebrush squirreltail (*Sitanion hystrix*) from Utah, plants processed by Ira Clark, Intermountain Forest and Range Experiment Station; blue grama (*Bouteloua gracilis*) from Colorado, processed by David F. Costello, Rocky Mountain Forest and Range Experiment Station; and Sandberg bluegrass (*Poa secunda*) from Utah, processed by Ira Clark.

The process of preparing height-weight tables consists of collecting ungrazed plants from the range, then cutting them at one inch or other convenient intervals from top to bottom, weighing the segments and converting this information into percentage height and weight.

Such height-weight tables were prepared for several species in Montana by Lommasson and Jensen (1938); in the Southwest by Crafts (1938); and in Utah by Clark. The original height-weight curves have been used in the field determination of utilization. However, Lommasson and Jensen, and

Crafts independently prepared gauges or "slide-rules" in which to carry the height-weight data in compact form and use it readily. The examiner measures both grazed and ungrazed plants of a selected key species, sets the ungrazed height in the gauge, and opposite the grazed stubble height reads the percentage utilization. In field practice, of course, this procedure requires measuring a representative sample. Reid and Pickford (1941) found that the height-weight and the ocular estimate by plot methods gave substantially the same estimates of utilization on grasses if the stubble height was rather uniform. However, they found the ocular estimate to be simpler in field use.

Still another method of determining range utilization is the measurement of stubble height along a line transect, used in research at the Southwestern Forest and Range Experiment Station (Canfield, 1941).

One final utilization method requiring mention is the visual evaluation of plant residue, developed for application on California annual type ranges (Hormay and Fausett, 1942). Since maintenance of soil fertility and forage productivity on this type depends upon a fairly complete plant cover, the relative amount of debris remaining after grazing is finished each year is judged ocularly. A particularly helpful criterion is the extent to which surface objects such as rodent mounds, pine cones, and sticks are obscured by the remaining vegetation. Systematic observation is, of course, necessary to secure average utilization over large pastures.

Regardless of method of determining utilization, the figure obtained on a range must be compared with a predetermined proper utilization percentage for the important forage species. Also very careful observation of soil erosion, disturbance, and range condition are necessary for an adequate picture of utilization and its effects on the range.

APPLICATION OF RESULTS

Out of all this complexity of factors, plant types, forage species, climatic variation, proper use, and methods of measuring utilization, must come a fairly simplified procedure for application in range management by the stockman and range administrator. One of the first tasks in the Forest Service range utilization study started in 1936 was the assembly of available utilization guides into practical regional handbooks, primarily applicable to national forest ranges. An example is the handbook prepared by Swift and Fausett (1939) for California ranges. After a brief background on range condition, this handbook presents writeups for each of several major types with photographic and text descriptions of the type itself, in good and in poor condition, overutilized and satisfactorily utilized. Research has since brought out several publications embodying useful standards. In addition to several already mentioned, important contributions include Costello (1942) on short-grass ranges of eastern Colorado; Campbell and Crafts (1939) on black-grama ranges; and Crafts and Glendening (1942) on blue-grama ranges of the Southwest. It has also been necessary to standardize and simplify certain concepts such as key areas, key species, and utilization in terms of percentage weight.

As a part of the Department of Agriculture program for sustained livestock production from western ranges, useful range research results have been furnished to range managers generally. Direct assistance has been given the Agricultural Adjustment Agency by preparing and adapting height-weight tables for attaining more efficient use of forage and better management generally on private ranges. Improved procedures have been furnished to range technicians of the Forest Service and other public agencies. Especial emphasis has been given the formulation of better proper use ratings for important forage plants under different sets of conditions. Sound proper use figures for the important forage plants are basic for effective range surveys and the subsequent application of good practices through carefully prepared management plans for range units. Finally a systematic effort has been made to show range managers all through the West that sustained production is obtained only conservative grazing on ranges in good condition.

FUTURE RANGE UTILIZATION RESEARCH

The present period of practical application of utilization standards for maximum wartime production of forage and livestock affords good opportunity to reanalyze the problem so that future research will be pointed at the most urgent features. Among these is a better evaluation of condition and trend to avoid the deterioration that has taken place in the past. A start on work of this sort was made by Ellison and Croft at the Intermountain Forest and Range Experiment Station in 1942, combining range ecology and watershed management viewpoints. A particular weakness is the lack of criteria for judging soil condition. In some instances the vegetation indicated satisfactory condition and trend at the same time that excessive trampling by livestock was causing abnormal erosion. These criteria will include such things as litter, bare soil surface, and top soil remains.

Utilization studies should be extended to additional types and species with special emphasis on deteriorated ranges in order to restore them to maximum productivity as quickly as possible. The effect on forage plants of utilization by big game and rodents is an important field in itself, still largely unexplored. More work along plant physiological lines is needed so that management can be based on a better knowledge of the internal processes of plants on grazed ranges. Gaps in present information are the mechanisms which enable some plants to better survive grazing and drought than others. Likewise, the entire utilization question needs a much better knowledge of ecology, particularly of the important forage plants in relation to the habitat. Finally, related work on nutritive values of forage plants is needed in order to secure the greatest livestock production from range lands in coordination with farm crops and other feed supplies.

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BOTANY.—*Distribution and character of* Sabal louisiana.[1] MIRIAM L. BOMHARD, U. S. Forest Service.

Sabal louisiana (Darby) Bomhard was described under the genus *Chamaerops* in 1816[2] by William Darby, but it escaped the serious attention of botanists until the spring of 1925, when the late Dr. John K. Small rediscovered it. He published it as a new species, *S. deeringiana*, in 1926,[3] for he was not then aware that an earlier name existed. In this paper Dr. Small pointed out that native arborescent palmettos were thought to be lacking along the thousand-mile stretch of the Gulf coast between St. Andrews Bay, Fla., the western limit of *S. palmetto* (Walt.) Lodd., and the lower Rio Grande River near Brownsville, Tex., where *S. texana* (Cook) Becc. is indigenous. The type locality is given as "Flat alluvial places, near Pointe aux Herbes, along Lake Pontchartrain, Louisiana."[4] This is indeed a very restricted area east of New Orleans and slightly northwest of the Chef Menteur (a pass between Lakes Pontchartrain and Borgne).

In a later paper, 1929, following further field work in the general region of Lake Pontchartrain and the Mississippi Delta, Dr. Small wrote: "The geographic limits of *Sabal deeringiana* are not yet perfectly known. It grows in swamps and along bayous in the lower Mississippi delta. It has not been observed east of the Pearl River, nor west of the Atchafalaya River."[5] In his *Manual of the southeastern flora* (1933), the distribution is given as "Flat alluvial places along the lower Mississippi River, bayous and lakes, S. La."[6]

About 1932 I began to make surveys of habitats similar to those in which Louisiana palmetto was rediscovered, as well as in areas mentioned by Darby. The results for Louisiana were published in 1935 and summarized in the following statement: "Although palmettos are widely distributed over much of eastern and southern Louisiana, they attain their most luxuriant development in the southeastern portion of the State, where trunked forms occur. Trunked palmettos are much more widespread in Louisiana at the present time than has been supposed, having been found by the writer westward nearly to Opelousas and south almost to the Gulf of Mexico."[7]

Emphasis was first placed on trunked palmettos because the climax form with a well-developed trunk is easily recognized. For example, the arborescent *Sabal louisiana* specimens standing fairly in the open at Frenier Beach on the west shore of Lake Pontchartrain are so different from other tree-Sabals that the distinctive characters of this species in its prime are unmistakable.[8] Then, too, the most logical approach to an understanding of any arborescent palm species in its native habitat is through observation of the developmental series of a population in the midst of obviously mature trees. Thus, it later became possible to ascertain the identity of groups of *Sabal louisiana* which had not yet attained their prime and with which mature trees were not intermingled.

From observations in Louisiana it seemed apparent that Louisiana palmetto would be

[1] Received March 22, 1943.

[2] DARBY, WILLIAM. *A geographical description of the state of Louisiana . . . being an accompaniment to the map of Louisiana*, ed. 1: 194. 1816.

[3] SMALL, JOHN K. *A new palm from the Mississippi Delta*. Torreya 26: 33–35. 1926.

[4] There are no Louisiana palmettos in the marshes in the immediate vicinity of Pointe aux Herbes. Those seen by Dr. Small were a distance south of this place.

[5] SMALL, JOHN K. *Palmetto-with-a-stem*—Sabal deeringiana. Journ. New York Bot. Gard. 30: 283. 1929.

[6] SMALL, JOHN K. *Manual of the southeastern flora*: 240. 1933.

[7] BOMHARD, MIRIAM L. Sabal louisiana, *the correct name for the polymorphic palmetto of Louisiana*. Journ. Washington Acad. Sci. 25 (1): 42. 1935.

[8] The only habit photographs of this species thus far published by others are of specimens at Frenier Beach. See Figs. 5 and 6 in SMALL, JOHN K. (1929), and Figs. 152 and 167 in BAILEY, L. H., *Sabal et ceterae*. Gentes Herbarum III, fasc. VI, art. 6, 1934. Dr. Small's Fig. 6 was republished in his article *Palms of the Continental United States*. Sci. Monthly 32: 10. 1931. A photograph of a specimen growing near Bayou Bienvenue, eastern Louisiana, was published as Fig. 1 in BOMHARD, MIRIAM L. *What palms grow in Louisiana*. Louisiana Cons. Rev., Autumn, 1937.

distributed throughout the Gulf Coastal Plain (including the Mississippi Alluvial Plain) wherever the physiographic and micro-climatic conditions are essentially the same. Exploration in this broader area, based on this premise, has been carried out since 1935—along the waterways of recent alluvial origin where conditions are reasonably similar to those of southeastern Louisiana and where it could almost be predicted that *Sabal louisiana* would occur.

As a result of these studies the present known range of *Sabal louisiana* has now been considerably extended. From Louisiana this species radiates out into eastern Texas, southeastern Arkansas, and at least into western Florida. The most important extension was the discovery of *Sabal louisiana* in Texas, where it had apparently not been previously observed by botanists.[9] The finding of well-developed arborescent palmettos in that State is especially significant and conclusive.

On a brief trip through eastern Texas in May and June of 1941, two stands of *Sabal louisiana* were discovered south of Cleveland, Tex.—on the western margin of the "Big Thicket." The first, in a local depression just below the town itself, consisted of a dense stand of palmettos, most of them in the intermediate growth stage, with a boot-aggregation of 40 cm or more, leaves 18 dm in expanse, and very robust, strongly branched inflorescences more than 45 dm tall although not yet in bud. This group is similar to many of those in southeastern Louisiana growing under the most favorable environmental conditions.

The second, 4 miles south of Cleveland, within sight from the bridge (U. S. Highway 59) that crosses the East Fork of the San Jacinto River, was a group with arborescent specimens. Perhaps 20 trees are easily accessible, scattered in a rather open portion of the flood bed on the east bank of the river. Farther back, in an area not readily accessible, the large crowns of many other Louisiana palmettos are visible. It was possible to take specimens, measurements, and photographs (Pl. 1, lower left) only of the trees in the open area. The trunk height of these did not exceed 11 dm, and the diameter, without boots, averaged 33 cm. This group is, in many respects, a replica of a stand in the Vermilion River bottomland, near Intracoastal City, southern Louisiana, where short-trunked palmettos remain in clearings nearest the newly made road and the more robust specimens are inaccessible in the midst of woody vegetation, subject to annual inundation.

Another collection of *Sabal louisiana* was found in the bottomlands of the Lavaca River, west of Lolita, Tex. Those nearest the road, although of intermediate character and of uniformly the same age, were so dense and the flood area appeared to be so broad that arborescent specimens in their prime or even old specimens might have been brought to light had there been time to give this region more than a cursory investigation.

Having seen some small groups of poor-looking palmettos (intermediate stage) near the Colorado River, in the vicinity of Wharton, and on the San Bernard River, near Hungerford (U. S. Highway 59), I later made a hasty survey of these same river areas nearer to the coast, this time following State Highway 35, that is, near Bay City and near West Columbia, and also out of East Columbia on the Brazos River. Although conditions here were favorable for arborescent palms, I did not find any in the limited time at my disposal.

However, at least one excellent stand with trunked palmettos does occur in the San Bernard River bottomland 8 miles from Brazoria, Brazoria County. Discovered by Robert A. Vines, of Houston, Tex., these palms were brought to my attention in June, 1942, by C. V. Morton, of the United States National Herbarium, to whom Mr. Vines sent photographs and notes, leaves, and portions of a fruiting stalk of an arborescent *Sabal* for identification. It proved to be *Sabal louisiana*. This discovery of a group of 20 or more of these palms is a fine contribution to the distribution pattern of *Sabal louisiana*, especially since three very old trees are in the group, one with a trunk

[9] See PARKS, H. B., CORY, V. L., and others. *Biological survey of the east Texas big thicket area*, ed. 1, 1936, and ed. 2, 1938. There is a photograph on page 24, captioned "Giant palmetto," but *S. minor* is the only species of this genus given (p. 33) in the list of plants of the big thicket.

height of 54 dm—the greatest height yet recorded for the bole of Louisiana palmetto. A portion of Mr. Vines's notes accompanying the specimens (*Vines* 425) reads as follows: "HABITAT.—Swampy black soil. Associated with *Sabal minor*, *Quercus virginiana*, *Ulmus crassifolia* and *Fraxinus pennsylvanica* var. *lanceolata*. REMARKS.—A palm with a distinct trunk. A handsome palm. Flowers in June and July. Fruit matures in November and December. Evidently very limited in distribution. Eighteen plants found within a half-mile radius. From the number of young plants seen, it was evidently reproducing itself satisfactorily. All the trees grow in thick tangles of vegetation, and are thus protected from excess cold during winter. Old settlers say this small isolated group of palms has been growing wild in the bottomlands as long as they can remember."

Mr. Vines has recently graciously supplied me with his negatives, from which the illustrations in the upper and lower right of Plate 1 were made, as well as with the following additional statement concerning the circumstances of his discovery and locality details:

> The stand of palms grew on the land of Deputy-Sheriff Harold Graves, of Brazoria, Tex. The stand is located on the Brazoria–Cedar Lane cut-off road approximately 2 miles east of the Brazoria and Matagorda County line. The Brazoria–Cedar Lane road runs through the center of the stand. When the road was built some of the workmen dug up some of the large specimens to plant in their yards. According to Deputy-Sheriff Graves and several other of the older settlers, the palms have been there for many years. They remember them as having been in that location for 25 or 30 years. They first remember them when squirrel hunting in the bottomlands as boys, and when rounding up cattle, before the road was ever cut through.
>
> I have also heard rumors of another stand of aborescent palms in the same region. The rumor circulated by old Negro settlers who said they used to see the big palms while fishing on the San Bernard River. None of them, however, could give me exact directions as to just where it might be. I tried several of the leads, but they always were blind ones. I still have a suspicion that at one time quite a large stand must have existed along the San Bernard River. This stand, of course, might have been destroyed, but the rumors, and stories of it, still exist. I still have hopes that I shall be able to rediscover the remnants of the stand eventually.
>
> I first saw these palms, that is, those on the Brazoria–Cedar Lane road, during the summer of 1941, but it was not until the summer of 1942 that I collected specimens and took pictures of them.

Doubtless other arborescent stands will be found in protected areas, where optimum conditions exist, in Texas and other portions of the Coastal Plain.

Louisiana appears to be the center of distribution. Observations thus far made indicate that the greatest concentration of vigorous and thriving stands, including many individuals of arborescent character, occurs in the fertile soils of the lower Mississippi Alluvial Plain. This is partly due to the fact that habitat factors are most favorable for their development and partly because much of this region—in the wetter areas—has not yet been too greatly altered by the destructive forces of man.

The phrase "flat alluvial places" does not, however, convey the true character of the habitat of *Sabal louisiana* even in southeastern Louisiana. Although the areas where it occurs are alluvial, they are not strictly flat. The topography is varied. Account must be taken of the paired alluvial or deltaic ridges, of greater or less width and elevation, that traverse the swamps, marshes, and other low-lying areas. The ridges were formed by alluviation from a series of successively developed distributary channels of the Mississippi River, most of which are no longer active. The land is highest nearest the active or abandoned channels of distributary streams, and slopes toward the wetter areas, characterized by temporary or permanent marshes, swamps, lagoons, or lakes. Louisiana palmetto frequently occurs in the so-called "back land" zone or belt between the ridgeland and the marshes or swamps; it may actually border the wet areas; or if the ridges are of low elevation, it may occupy the ridges themselves usually forming an understory to the other arborescent vegetation. It also occurs in coulees or relict distributionary channels. It is at its best in the mild climate of the Gulf coast, where there is a high water table for much of the year and where partial shade is provided by the surrounding vegetation. It is not a "swamp plant" in the

sense that baldcypress and water tupelo are considered to be swamp trees.

S. louisiana also occurs in the valleys of the Red and Ouachita Rivers, as well as in the Mississippi flood plain proper, where artificial levees and spillways hold the floods in check. In *Louisiana out-of-doors* Percy Viosca, Jr., writes concerning the large interior river valleys, that include hardwood valley lands, river basin swamps, and lakes above Gulf level: "As this region is the richest in the state from an agricultural standpoint, most of it has been cut over, and in place of the forests, today we find sugar cane, corn or cotton fields and truck and dairy farms. Cane is raised more toward the southern part of the state, and cotton more in central and north Louisiana."[10] He states further that palmetto thickets and canebrakes occur on alluvial and "bluff" soils wherever the water table is near the surface.

There is every indication that *S. louisiana* formerly occupied a much larger area than it does today and that there were countless more individuals of tree size. Indeed, William Darby wrote 137 years ago: "The land is commonly of the best quality. Much of the surface of the country low upon the Mississippi, now cultivated in cotton, maize, rice, and sugar, was originally covered with palmetto."[11] Extensive engineering operations, including the building of artificial levees, the closing off of certain natural waterways, the construction of roads, accompanied by clearing of the vegetation and digging of drainage ditches and canals with consequent lowering of the water level, the reclamation of land for cultivation—all have contributed to the disappearance of these palmettos.

This destruction may be witnessed today. The illustration in the upper right of Plate 2 shows the effect of road-building near Intracoastal City, Vermilion Parish, La. The area here occupied by Louisiana palmetto is still rather extensive but it was previously in much more flourishing condition. Dead trunks are lying about on the ground as the result of burning and clearing, and many palms that are still living show charred trunks. The one-time height of the flood level in this area may be noted from the root zone on the trunk just below the "boots" of the small tree illustrated. Fortunately, a distance back of the road, arborescent specimens in their prime with inflorescences overtopping the surrounding vegetation still exist.

The illustration in the upper left of Plate 2 shows a specimen with medium-sized trunk in what was, until a few years ago, a lovely grove of Louisiana palmetto, lying between a natural levee and a cypress-tupelo swamp, near the eastern limit of New Orleans. Many palms were destroyed by clearing and burning, in the process of extensive road-construction and draining, in the general area of Bayou Bienvenue. More recently truck gardening has been initiated in the rich soil of this area, in the midst of chopped and burned palmettos.

In a report of a survey of the Rio Grande River in Texas, Arthur Schott made the following reference, in 1859, to a "gorgeous" growth of palmettos on the Mississippi River: "It is also in the lower portion of this belt (where the Palm tribe is represented by the Chamaerops Palmetto) that the Palmetto attains a growth as gorgeous even as that on the Lower Mississippi; it extends on the Rio Bravo [Rio Grande] up to about 80 miles from the Gulf. In addition to the Palmetto common to the lower portion of these two great rivers, . . . "[12]

In calling attention to Schott's statement, Dr. Small commented: "Field work in the lower Mississippi delta by the writer subsequent to the spring of 1925, has convinced him that the extensive engineering operations connected with the building of the levees along both banks of the river utterly exterminated the palm growth referred to by Schott. Arthur Schott made his observations about the middle of the last century, while extensive levee building occurred about the beginning of the last quarter of that century. It is evident that neither the engineers in charge of the levee work nor

[10] VIOSCA, PERCY, JR. *Louisiana out-of-doors: A Handbook and guide*: 51. 1933.

[11] DARBY, *op. cit.*

[12] SCHOTT, ARTHUR. *Substance of the sketch of the geology of the lower Rio Bravo del Norte*, pt. 2, *in* Emory, William H. *Report on the United States and Mexican boundary survey* 1: 44. 1857.

their associates were botanists, else some record additional to Schott's original statement would have found its way into print."[13] It should be mentioned here that even near the Mississippi itself a few trunked trees of *S. louisiana* occur south of Buras; they have very small crowns and are not now growing in a very favorable situation. Furthermore, the Mississippi Delta occupies a widespread area, and it can be seen from the outline map (Fig. 1) that there are still groups of Louisiana palmetto in many portions of it.

Forty-three years before Schott published the statement quoted above, Darby wrote: "Along both banks of New River, in the rear of the plantations on the Mississippi, and on the banks of the Atchafalaya, are the places where most of the arundo [*Arundinaria gigantea*] yet exists. Here, as well as in every other part of Louisiana, where the land sinks too low for the arundo, is found the *Chamaerops louisiana*.[14]

At the present time, there is still a good representation of Louisiana palmettos between Gonzales, just south of New River, and Sorento, in Ascension Parish. In the lower Atchafalaya Delta arborescent specimens of *S. louisiana* may also be seen today near Morgan City and east of it along Bayous Black and Chacahoula.

Darby described Louisiana palmetto as a new species because he was of the "opinion that there is a specific difference between the *Chamaerops palmetto* hitherto known to botanists, and that of Louisiana."[15] The mistake of Schott, Langlois,[16] Featherman,[17] and others of thinking that Louisiana palmetto was the cabbage tree, *S. palmetto* (=*Chamaerops palmetto* Michx.), does not seem to me to indicate such a serious error in judgment on the part of these observers, but it does show the astuteness of Darby. Certainly this palm could not be the stemless *S. minor* (Jacq.) Pers. To what other arborescent palmetto could it have been referred, considering that Darby's work and publication was apparently not well known and that *S. texana* had not yet been described?

Natural factors also are contributing to changes in the aspect and extent of Louisiana palmetto stands or to their complete obliteration. Two examples—the first on the southwest; the second on the north, shore of Lake Pontchartrain—are of interest. Many of the taller palmettos in the striking group of 35 or more at Frenier Beach (west shore) (2),[18] standing in a coulee back of the lake shore, give the appearance of having been planted for ornamental purposes. There are few transitional forms in this relatively open area, but all stages of growth occur in the low ground to the rear. This beach was built by alluvial deposits; there is a clay base, which, until quite recently, was overlaid with sand. The shore is now being cut back at a rapid rate, geologically speaking. Continued erosion will in the future change the natural habitat. The character and relative abundance of the palms will also be altered as a consequence.

On the north shore, just east of Mandeville (5), a later stage in the squence is taking place. Here the lake, brackish at times, is encroaching upon the land and has already built up a sand ridge, 8½ feet in height, upon the shore. Similar sand-encroachments are taking place in certain other portions of the north shore of Lake Pontchartrain. The extent of swamp was formerly much greater, as attested by cypress stumps about 400 feet out in the lake and dead or dying cypress trees standing at the water's edge. A direct line from the outer margin of the cypress swamp into the lake passes in succession (1) Louisiana palmettos in flourishing condition but with an inconsiderable development of trunk; (2) specimens almost completely buried in the sand, so that only the upper portion of their trunks and crowns is free; and (3) arborescent palmettos standing in a foot or

[13] SMALL, JOHN K. *Palmetto-with-a-stem*—Sabal deeringiana. Journ. New York Bot. Gard. 30: 280–281. 1929.

[14] DARBY, *op. cit.*, 193–194.

[15] *Ibid.* 194.

[16] LANGLOIS, A. B. *Catalogue provisoire de plantes phanérogames et cryptogames de la Basse-Louisiane, États-Unis d'Amérique*: 17. 1887.

[17] FEATHERMAN, A. *Report of botanical survey of southern and central Louisiana made during the year 1870*: 25. 1871.

[18] The figures in parentheses in the text refer to localities on the outline map (Fig. 1).

more of water out in the lake itself. The crowns of the palmettos in the last two groups are much reduced in size, the leaves are thick and very filiferous, and the flowerstalks are telescoped. Eventually this whole stand will be no more, even though new plants will for a time continue to come up between the ridge and the ever-shrinking cypress swamp.

Dr. E. W. Berry states that "the silicified remains of palm wood are exceedingly common in the late Eocene and Oligocene deposits from Texas eastward across Louisiana, Mississippi, and Alabama, and reappear in several of the Greater and Lesser Antilles, as well as in Mexico and on the Isthmus of Panama."[19] Palm leaves are also preserved in certain of these deposits. Various genera are represented, but the correlation of fossils with living genera or species can only be approximate. In the palm family, leaf remains naturally provide more useful identification characters than trunks.

There are fossil deposits containing leaves and "rays" (segments) of *Sabal*-like species in the Jackson formation (Upper Eocene), especially in the Vicksburg limestones and Catahoula and Fayette sands, from eastern Texas to Georgia. Beds of Vicksburg age are notable for the abundance of palm fragments and are of especial interest. The fossil leaf species, *Sabalites vicksburgensis* Berry,[20,21] is described as having a maximum expanse of 120 cm, the rachis continues upward part way through the blade, and the 40 segments, up to 3.6 cm wide, become free in the outer one-third to one-half of the blade. Although the type locality of this fossil species is Rosefield, La. (Catahoula sandstone), it is also abundantly represented in sands of similar age in Fayette, Polk, Trinity, and Webb Counties, Tex. Certain other species of *Sabalites* seem to indicate close relationship with *S. palmetto* or with *S. minor*; it is not improbable that *Sabilites vicksburgensis* may represent an ancestor of *S. louisiana*, which certainly must have been more widespread in geologic time.

Louisiana palmetto, like other species of *Sabal*, evidences a wide range of adaptability to various environmental conditions and, in common with many palms, has different aspects from youth to old age. A consideration of it in four ontogenetic stages—juvenile, intermediate, climax or mature, and senescent—should contribute to a better understanding of this species.

Apparently there are comparatively few senescent Louisiana palmettos in existence, and all that I have seen in Louisiana are, or appear to be, growing in habitats that are no longer entirely favorable. Only an approximation of their age is possible but it is known that this species grows slowly. An ancient tree, such as that illustrated in the upper left of Plate 1, may well be 200 or more years of age. Four (occasionally eight) leaves are produced by *S. louisiana* in a season; the leafscars on the trunk are very close together. It is not determinable what length of time elapses in the production of the horizontal underground stem before the erect habit is assumed.

A reduced leafcrown—smaller blades on shorter petioles—and shortened, telescoped inflorescences are indications of senescence or induced senescence. Thus, the total height of an old specimen with relatively tall trunk is often less than that of a specimen in its prime with much shorter bole. The more robust appearance of the younger palmettos in the photograph is evident as is also the contrast between the senescent tree and the young climax form at the left.

This group (Pl. 1, upper left) is part of the largest single Louisiana palmetto area of which I am aware, but I have not seen more than a half-dozen senescent specimens in it. Thousands of palmettos, the majority in the intermediate and climax stages, occupy an almost unbroken stretch of at least 20 miles from Golden Meadow to a distance south of Leeville, La., along Bayou Lafourche (14). This bayou no longer functions as a distributary of the Mississippi River, having been closed off from it in 1912. The broader alluvial regions in the upper por-

[19] BERRY, E. W. *The flora of the Catahoula sandstone.* (M) in *Shorter contributions to general geology*, 1916. U. S. Geol. Surv. Prof. Paper 98: 233. 1917.

[20] *Ibid.*

[21] BERRY, E. W. *The Middle and Upper Eocene floras of southeastern North America.* U. S. Geol. Surv. Prof. Paper 92: 151, pl. 29. 1924.

tion of its course are under cultivation. The palmettos are to be seen in the lower portion. They occupy a relatively narrow, almost treeless zone between the ridge-road and swamp or marsh, or they occur as an understory on the chéniêres. These ridges near the coast, on which live oak (*Quercus virginiana*), water oak (*Q. nigra*), and hackberry (*Celtis laevigata*) form the dominant vegetation, take their name from the French *chéne*, oak. The palmetto growth fades out together with the diminishing chéniêres toward the Gulf of Mexico.

The few senescent specimens in this large tract closely resemble each other; some have more boots clinging just under the crown. A dense mass of roots clothes the lower 4.5 dm or less at the base of all of them. The trunks are almost white—a modification in this saline situation, where the insolation is intense, of the normally grayish-brown tone of the bark of this species. The longitudinal fissures that cross the closely spaced leafscars lend a checkered appearance to the bark.

In Louisiana old palmetto individuals also occur near Bayou Bienvenue (3) and near the Mississippi River on Bayou Laird, south of Buras (15); the trees, partly buried in the sand ridge on the north shore of Lake Pontchartrain (5) and with only 75 cm of visible trunk, are also senescent. Measurements in these scattered localities are very similar and may be summarized as follows: TRUNK: Height, 15–26.5 dm (up to 54 dm in Texas); diameter of trunk devoid of boots, 22.6–28 cm. LEAF BLADE: Expanse, 10.5–13 dm; length in middle line, 6.5–9 dm; rachis length, 15–26 cm; number of segments, 34–40; widest segments, 3.8–5.7 cm; sparsely to very filiferous in the sinuses, depending upon the habitat. PETIOLE: Length, 50–80 cm; width near blade, 2.2–2.9 cm; width near base, 2.8–3.8 cm. INFLORESCENCE: Height, 12–27 dm; width at base of inflorescence stalk, 3.2–7.6 cm; number of sterile spathes, 10; number of fertile spathes, 7–13.

The specimen illustrated in the upper right of Plate 1 was photographed by Mr. Vines in the San Bernard River bottoms (28) of Texas. Three trees in this area are old, the tallest trunk measuring 54 dm. The diameter averages 30 cm. This locality appears to represent a more nearly normal habitat for *S. louisiana* than any of the areas in Louisiana where old trees have been observed. The crown shows reduction in size, but the leaves appear to be larger and the petioles are longer than those whose measurements have just been listed. This is to be expected where palms occur in an undisturbed wet area in "thick tangles of vegetation." Sudden lowering of the water table has apparently not occurred in this region and it is probable that complete drying out of the terrain does not take place. This venerable group should continue to be protected. It is highly desirable that certain groups of Louisiana palmetto in Louisiana should be set aside for conservation, inasmuch as stands of this sort are imminently threatened with extinction.

Louisiana palmetto evidences the full vigor of maturity in the climax stage. The few descriptions of this species thus far published apply, with some emendations, to this life-form. Ordinarily the climax stage is a bulky palm, with heavy, impressive crown, but its appearance varies somewhat with habitat just as do other phases of this species. Plate 1, lower left and lower right, illustrates typical specimens in Texas (27 and 28). The most typical specimens in

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PLATE 1.—Upper left: Senescent *S. louisiana*, surrounded by palmettos of intermediate growth stage with boot-aggregation, and young climax forms with short trunks such as that to the left of the old tree. In an open situation where the habitat is no longer entirely favorable, along Bayou Lafourche, near Leeville, La. (15).

Upper right: Senescent *S. louisiana*, with trunk height of 51 dm. In an apparently optimum habitat, San Bernard River bottoms, 8 miles west of Brazoria, Tex. (29). Photograph by Robert A. Vines.

Lower left: Louisiana palmetto of climax form. Upper portion of trunk and lower part of crown. Open bottomland, East Fork of the San Jacinto River, south of Cleveland, Tex. (27).

Lower right: Vigorous climax specimen that has retained the leaf bases in a favorable, protected habitat. Mr. Vines, who discovered and photographed this stand, is holding a leaf cut from a younger climax palmetto growing nearby. San Bernard River bottoms, 8 miles west of Brazoria, Tex. (29).

PLATE 1.—(See opposite page for explanation.)

PLATE 2.—Upper left: Typical young climax form of *S. louisiana*. Near Paris Road, vicinity of Bayou Bienvenue, La. (3).

Upper right: Climax Louisiana palmetto, showing the effects of burning and clearing in connection with road-construction. Sawed palmetto trunks in the left foreground. Near Intracoastal City, La. (16).

Lower right: "Field type" of intermediate growth stage, showing the characteristic collapse of the dying leaves. Along a fence bordering a cottonfield, Rayville, La. (35).

Bottom: A group of palmettos in intermediate growth stage toward the northern limit of the range of *S. louisiana*. The strongly branched inflorescences are not yet in bud (May 23, 1941). West of Montrose, Ark. (23).

southern Louisiana, such as that shown in the upper left of Plate 2, grow in partial shade on moist fresh-water sites that are flooded in winter and in early spring. In the lower-lying areas Louisiana palmetto is associated with willows (principally *Salix nigra*), red maple (*Acer rubrum drummondii*), and ashes (*Fraxinus caroliniana*, *F. tomentosa*, or *F. pennsylvanica lanceolata*), not far removed from the deeper swamps dominated by baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*, usually known as tupelogum) or swamp blackgum (*N. biflora*). On the ridges, dominated by live oak and hackberry and sometimes also southern magnolia (*Magnolia grandiflora*), the other arborescent associates of Louisiana palmetto include American sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), willow oak (*Q. phellos*), waterelm (*Planera aquatica*), and American hornbeam (*Carpinus caroliniana*). Common honeylocust (*Gleditsia triacanthos*) or yaupon (*Ilex vomitoria*) is also frequently present.

In the interior river valleys of central and northern Louisiana tree communities of the wetter areas are, on the whole, similar to those farther south. Several additional species of oak, such as red oak (*Q. shumardi*), Nuttall oak (*Q. nuttalli*), and overcup oak (*Q. lyrata*), pecan (*Carya pecan*), winged elm (*Ulmus alata*), and other hardwoods augment the list of tree associates that occur with Louisiana palmetto on the ridgelands farther from the coast.

In optimum habitats a characteristic specimen of Louisiana palmetto with medium-sized trunk has large, comparatively thin, bluish-green leaves up to 20 dm broad. The length in the middle line is 9 dm or more; but this is somewhat shorter than the maximum blade length in either side of the center. The pinnati-palmate leaves are not in one plane. The blades have a characteristic "palmetto-curve," but it is not so strongly developed as in *S. palmetto* and other large-leaved arborescent Sabals. The rachis (continuation of the petiole as a midrib into the blade, along which most of the segments originate) is winged below and firmly supports the lower one-third of the blade, but, beyond it, the leaf is deeply split into two halves. From 36–50 segments divide the outer half or two-thirds of the blade, the inner solid portion being broadly heart-shaped in outline with the notch at the top, at the end of the rachis. The broad, gradually acuminate segments stand out rather stiffly; their apices, although bifid from several to 13 cm (or even more at the sides), are usually not flaccid. A thread-like fiber hangs in the clefts of the younger leaves but only a few persist in older ones. The flat, platelike hastula, at the juncture of the petiole and blade on the upper surface of the leaf, is asymmetrical and averages 4 cm in length.

The unarmed petioles, longer than the blades, are concave on their upper and rounded on their lower surfaces; the upturned margins are very sharp, faintly denticulate toward the base. The peitole bases split with age but only occasionally form a crisscross or lattice (so characteristic of the larger *Sabal* species). The two boot-halves remain erect or at least ascending for a considerable period. The sheaths are never prominent; in fact, they are noticeable only in the youngest part of the crown, where the petiole bases of the newest leaves are bordered by narrow, chaffy, light brown margins.

One of the most interesting characteristics of this species is the peculiar collapse of the dying leaves at the juncture of the petiole and blade, giving the effect of a half-closed umbrella. The blade may fall off at this point, or the petiole may break midway before the blade falls.

A trunk averaging 9–18 dm in height usually exhibits three zones: a region of roots at the base, a narrow girdle of bark, and a boot area below the leafcrown. Occasionally an additional root development occurs fairly high up on the trunk, indicating some previous high water level. (Compare the illustration in the upper right of Plate 2 with that in the upper left.) The actual trunk diameter (bark only) rarely exceeds 33 cm and is usually somewhat less. When the boots persist over a period of years, as often happens in the wetter situations, the trunk appears to be twice as thick as it actually is. The rough bark is usually grayish brown.

Four to six (generally four) inflorescences ("spadices" of literature) are produced in a season. They stand stiffly erect and, in the more open situations, may surpass the associated small trees. Twenty-two or more tubular, long-pointed spathes overlap each other and cover the length of the inflorescence axis. Those in the lower stalklike portion of the axis are sterile; the upper, fertile. *S. louisiana* is characterized by a thrice-compound inflorescence—the strongly developed, ascending or appressed, lateral branches that emerge from the lower fertile spathes may attain 9 dm in length in the climax form. The branches become progressively shorter until, toward the apex of the main inflorescence, the panicles emerge directly from the uppermost fertile spathes. The lower branches have five or fewer sterile spathelets at their base and the ten or fewer panicles are subtended by the upper fertile spathelets.

The young inflorescence shoots are visible in the leafcrown in November. These are elongated, attenuate-coniform structures, imbricated with the appressed apices of the lower spathes. Full development is not attained until the following spring. Flowering begins in June, or even late in May, and sometimes continues into July. In some years full flowering fails to take place, even on perfectly vigorous specimens, because of unusual infestation of the panicle buds by insect larvae. Some of the lower panicles of the branches may come into flower but the remainder are aborted. In 1933 only one palmetto tree in a stand of 40 or more bore normal inflorescences.

The flowers are white, sessile, 5–6 mm high, spirally placed about the rachillae at rather regular intervals, spaced several millimeters apart. They are subtended by two unequal bracteoles, the base of the smaller being partially enclosed by the larger. Floral characters are: calyx 2–2.5 mm high, cylindric and thick below, 3-angled, with three short, triangular, unequal, slightly carinate, thin, nerved lobes; corolla more or less united with the stamens into a short pseudotube at base; petals 3, broadly ovate, 3.3–3.5 mm high, 2 mm broad at base, thin, involute, minutely serrulate, thickened and hooded at apex, auricled at based, 5–7 nerved; stamens 6, the alternate shorter than the opposite that are adnate to the petals; filaments subulate-lanceolate, dorsoventrally flattened; opposite stamens 4.5–5 mm high, the filaments 4 mm high, 1 mm broad at base; alternate stamens 4–4.5 mm high, filaments 3.5 mm high, less than 1 mm broad at base; anthers bright yellow, introrse, short-sagittate, 1–1.2 mm long, anther sacs somewhat unequal; pistil comprised of 3 carpels, 3.5–4 mm high, 1 mm or more broad at the enlarged ovarial base, stylar portion 3-angled, apex truncate. The flower buds show 18 chromosomes (plate stage).[22]

The fruits are suborbicular, brownish black drupes, ripening in November. They average 9–11 mm in diameter and 8–9.5 mm in height. The reddish brown, sub-lustrous seeds, enclosed in a thin integument, are 8–9 mm in diameter and 6–7 mm in height. The micropyle is lateral.

Many of the fine groups of climax specimens along Bayou Sauvage and near the Chef Menteur (1 and 4), including some of those on which Dr. Small based his original description of *S. deeringiana*, are, unfortunately, no longer extant. However, favorable localities in Louisiana where numbers of characteristically well-developed climax specimens may still be observed are at Frenier Beach (2), near Bayou Bienvenue (3), in the lower portion of the Vermilion River bottom (16), along Bayou des Allemands (11), east of Berwick Bay on Bayous Black and Chacahoula and south of it on Bayou Shaffer (15), and in some other places (1, 12, 14). Fairly isolated individuals in their prime, noted in Louisiana, near the towns of Bunkie (19), Denham Springs (17), and Rayville (22), will be discussed in connection with Louisiana palmettos of intermediate growth stage. In Alabama a good stand of representative Louisiana palmettos grows in the bottomland of the Tensas River at the head of Mobile Bay,

[22] Dr. A. E. Longley, U. S. Department of Agriculture, obligingly examined many samples of Louisiana palmetto flower buds that had been collected in various localities. Only those from the Chef Menteur area along Bayou Sauvage proved to be in the proper stage for chromosome counts. They were collected from both climax and intermediate forms of *S. louisiana*.

in a locality inaccessible except by descent from the Louisville & Nashville Railroad trestle (24). The best groups thus far discovered in Texas have already been mentioned as occurring in the bottomland of the East Fork of the San Jacinto River (27) and in that of the San Bernard River (28).

Measurements of the climax form may be stated as follows: TRUNK: Height 9–19.5 dm; diameter of trunk devoid of boots, 28–34 cm. LEAF BLADE: Expanse, 16.5–20 dm; length in middle line, 9–12 dm; rachis length, 25–42.5 cm (usually 30–37.5 cm); number of segments 36–50 (usually 38–42); widest segments, 4.7–7 cm; usually sparsely filiferous. PETIOLE: Length, 70–145 cm (usually 105–135 cm); width nearest blade, 2–3.8 cm; width nearest base, 4.5–5.7 cm. INFLORESCENCE: Height, 25.5–39 dm (usually 36 dm); width at base of inflorescence stalk, 4.5–6.4 cm; number of sterile spathes, 10–14; fertile spathes, 12–18; lower inflorescence branches up to 9 dm in length.

Deviations from the characteristic climax form of the shaded, fresh-water sites are especially apparent in the extensive Bayou Lafourche palmetto area (14), evidencing adaptation to a different set of environmental factors. The leafblades are thicker in texture, glaucous, stiffer, yellow- or gray-green, and abundantly filiferous; the inflorescences average 30 dm in height; and the trunk diameter is not quite 28 cm.

Under favorable conditions there is a natural transition from the climax form to those of intermediate stage. It is so gradual that the line of demarcation has been arbitrarily placed to include in the intermediate stage those specimens whose trunks usually retain the leafbases to form "boot-aggregations" of 9 dm or less, and that do not yet show a true bark area. There is also no visible root development above the ground level. The leafblades are borne on longer petioles and are frequently larger than those in the climax form; they are ordinarily 3 dm broader in proportion to their length. The tallest inflorescences with the most strongly developed lower branches (up to 15 dm in length) also occur in this stage.

Palmettos of this robust intermediate stage occur in most of the optimum areas already given for the climax form. However, certain additional localities in which the palmetto population is predominantly or entirely composed of flourishing specimens in this and juvenile stages are of interest. These palmetto areas are indicated on the outline map by numbers 6, 7, 8, 9, 13, 18, 20, and 21 for Louisiana, 23 in Arkansas, and 26 and 29 in Texas. There is the possibility, of course, that climax forms are associated with the intermediate forms in the more inaccessible wetter portions of some of these areas but have not yet been discovered. In other populations, it is known that the larger palmettos were removed in the clearing of the forests for cultivation of sugar, cotton, or other crops. Where cultivation was later abandoned and the areas permitted to return undisturbed to forest, second growth timber has come in. In such places, provided that the water level is still near the surface, all the palmettos are of normal intermediate or younger growth stage.

Louisiana palmettos of the intermediate growth stage in normal environments have the following dimensions: TRUNK: Height, 3–9 dm. LEAF BLADE: Expanse, 12–21.5 dm; length in middle line, 8–11 dm; rachis length, 16.7–42 cm; number of segments, 34–50 (averaging 34–42); widest segments, 2.2–6.7 cm; sparsely to moderately filiferous. PETIOLE: Length, 95–160 cm; width nearest blade, 2.5–4.5 cm; width near base, 3.2–5.7 cm. INFLORESCENCE: Height, 27–46 dm; width at base of inflorescence stalk, 3.8–6.4 cm; number of sterile spathes, 9–11; number of fertile spathes, 11–17; length of lowest branch, up to 15 dm.

An unfavorable environment is reflected in the character of intermediate-stage palmetto groups subjected to adverse natural factors such as saline or brackish water, excessive direct sunlight, and the piling up about the plant bases—or removal therefrom—of soil and inundation debris. The great majority of the Louisiana palmettos of intermediate stage that grow in deep muck in exposed brackish habitats along Bayou Lafourche (14), some of those on the lake side of the sand ridge at Lake Pontchartrain (2), and the few specimens in sand on the east shore near the mouth of the Escam-

bia River, Fla. (25), show the effects of naturally trying conditions and closely resemble each other.

The character of Louisiana palmettoes in or near pastures, cultivated fields, or fields turned back to pasture is also associated with unfavorable environmental conditions, but these have been mainly brought about by the clearing of forests together with lowering of the water level, plowing or other methods of cultivation, and cattle-grazing. High insolation and long dry periods following brief or only occasional high water levels are contributing adverse factors. In the more northern latitudes the cooler winter temperature also exerts a retarding influence upon growth.

The growth form of all these palmettos in the intermediate stage is compact—the crown is less open and smaller than in those in optimum habitats, and the aggregation of boots at the base is very dense, probably because elongation of the upright trunk proceeds very slowly. The "palmetto-curve" of the thick, more or less glaucous, yellow- or gray-green, abundantly filiferous leaves is more prominent, as is the inclination of the two halves of the blade away from the middle line. The segments are relatively wider in proportion to the size of the blade. The characteristic umbrella-collapse of the dying leaves is pronounced (Pl. 2, lower right). From a distance, pastures and cut-over areas of palmettos resemble fields of shocked wheat. The thick, branched inflorescences are shortened and compressed, often being very similar to those of senescent trees. The lower branches are so close together in many of the field and pasture palmettos that the inflorescences have a bushlike appearance. Failure to develop inflorescences is not infrequent in palmettos that are exposed to grazing, plowing, etc., but those along fence rows and the margins of fields that border woods succeed in putting forth inflorescences in occasional years, if not annually.

Although the palmettos in naturally adverse habitats (2, 14, and 25) have somewhat larger leaves and boot-aggregations (3–6 dm) in contrast to the smaller leaves and boot-aggregations (about 3 dm) of the intermediate stage of fields and pastures (30, 31, 32, 33, 34, 35, 38, 39), the overall dimensions fall within the same range: TRUNK: Height of boot-aggregation, 3–6 dm. LEAF BLADE: Expanse, 12–15 dm; length in middle line, 6.7–9.2 dm; rachis length, 13–22 cm; number of segments, 32–40 (usually 32–38); widest segments, 3.8–5.7 cm; very filiferous. PETIOLE: Length, 45–95 cm; width nearest blade, 2–4.5 cm; width near base, 2.8–5.7 cm. INFLORESCENCE: Height, 20–28.5 dm; width at base of inflorescence stalk, 3.2–5 cm; number of sterile spathes, 9–12; number of fertile spathes, 10–17; length of lowest branches, up to 4.5 dm.

The palmettos, with boot-aggregations and branched inflorescences, that grow in certain cultivated alluvial areas of Louisiana have not previously been identified as *S. louisiana*, but they represent an intermediate stage just as surely as do the luxuriant specimens of intermediate form in favorable localities where the relationship is more obvious.

The stocky specimens growing in the open in pastures or abandoned fields, especially in central and northern Louisiana, frequently occur in large numbers. A succession to more vigorous palmettos of intermediate stage but still of the "field type," may sometimes be traced from these open palmetto areas to the lower-lying, wetter margins of the pastures or fields, neighboring woodlands, or up to the edge of small streams.

The discovery of three arborescent palmettoes in widely separated localities in Louisiana, where most of the surrounding countryside has long since been cleared and put under cultivation, not only suggests that arborescent Louisiana palmettos were formerly more common than now, but also, in my judgment, has a vital bearing upon the relationship of the intermediate-stage palmettos that grow in pastures and fields.

The first of these three individuals occurs in a deep woods just east of Denham Springs (17). When I last saw it several years ago, the trunk height was 14 dm, the leaves were 13 dm broad, and the inflorescences attained 36 dm in height—a typical climax specimen. It grew near a bayou branch of the Amite River that is consider-

ably lower than the highway along which intermediate-growth palmettos of the "field type" occurred.

The second lone individual of tree size has a trunk height of 13.5 dm, and a diameter of 29 cm. It grows in the water of a small coulee that courses through a pasture and is visible from the road (U. S. Highway 71), south of Bunkie (19). This specimen was flanked at the water's edge by other Louisiana palmettos of intermediate stage in good condition, but the palmettos ranging into

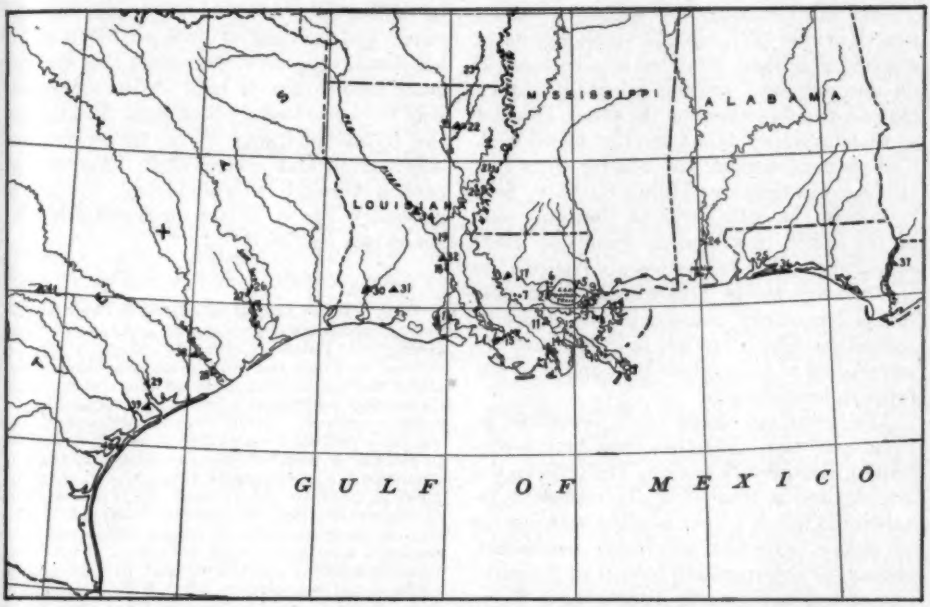

Fig. 1.—Distribution of *Sabal louisiana*. The dots on the map represent the more significant and typical stands or individuals of senescent, climax, or intermediate growth-form in the following localities: LOUISIANA—1, Along Bayou Sauvage, north of the Chef Road. 2, Frenier Beach, west shore of Lake Pontchartrain and northwards between Lakes Maurepas and Pontchartrain. 3, Near Paris Road, New Orleans, and the general vicinity of Bayou Bienvenue. 4, Along Bayou Sauvage, from Micheaud to the Chef Menteur Pass. 5, East of Mandeville, north shore of Lake Pontchartrain. 6, Manchac and other stations on the northwest shore of Lake Maurepas. 7, Between Gonzales, along New River, and Sorrento. 8, West of Shell Beach (on Lake Borgne) along Bayous Ysclosky and La Loutre. 9, West Pearl River, near Indian Village. 10, South of Buras and not far from the Mississippi River, vicinity of Bayous Grand Liard and Petit Liard. 11, Bayou des Allemands, near Des Allemands Station. 12, Bayou Villars, near the upper end of Bayou Barataria. 13, Bayou Dupont. 14, From Golden Meadow to a distance below Leeville, along Bayou Lafourche. 15, East of Berwick Bay and Morgan City along Bayous Black and Chacahoula (Chacahoula swamp), and southward along Bayou Shaffer. 16, Near Intracoastal City, Vermilion River. 17, East of the Amite River along a small bayou near Denham Springs. 18, Between Port Barre and Opelousas, in the vicinity of Bayou Teche. 19, Eight miles south of Bunkie. 20, Near the Tensas River, 8¼ miles west of Ferriday. 21, North of U. S. Highway 65, northwest of St. Joseph. 22, East of Rayville. ARKANSAS—23, Bayou Bartholomew, west of Montrose. ALABAMA—24, Tensas River delta north of Mobile Bay, west of Hurricane. 25, Eastern shore of Escambia River, at head of Pensacola Bay. TEXAS—26, East of U. S. Highway 59, just south of Cleveland. 27, East Fork of the San Jacinto River, about 4 miles south of Cleveland. 28, San Bernard River bottom, 8 miles west of Brazoria. 29, Lavaca River bottom, west of Lolita. The solid triangles indicate large groups of the "pasture or field type" (intermediate stage); the cross-hatched triangles, palmettos of reduced "field type" that require further study: LOUISIANA—30, West fork of Calcasieu River, near Westlake. 31, Near Welch, not far from Bayou Lacasine. 32, An area roughly bounded by Beggs, Palmetto, and Port Barre. 33, Between Comite and Puckett. 34, Between Bayou Boeuf and the Red River, near Alexandria. 35, Various localities, near Rayville. FLORIDA—36, Near Holley, south of the Yellow River. 37, Apalachicola River, east of Blountsville. TEXAS—38, San Bernard River, north of Hungerford. 39, Hog Bayou, about 8 miles south of Port Lavaca. 40, North of Rockport, eastern shore of Copena Bay. 41, On the Blanco River, south of Blanco. Map prepared by Leta Hughey.

the pasture had only short boot-aggregations and diminished crowns. Willows, a few baldcypress trees, American honeylocust, and giant cane are associated with them in the pasture. The large baldcypress trees at the margin of an extensive swamp can be seen in the distance.

The third arborescent specimen occurs near Rayville (22), along a small stream in a mixed woodland, bounded by a cottonfield on one side and passing gradually into a cypress-tupelo swamp on the other. It is not so well developed as the two just mentioned. The palmettos along the nearby fence row (Pl. 2, lower right) are of intermediate "field type." In the cottonfield on the other side of the fence row, and in countless areas round about, the palmettos are regarded as troublesome weeds. Following plowing, cotton is frequently planted in the midst of palmettos, which are not only low and impoverished in appearance but unable to put forth inflorescences.

The complete range of *S. louisiana* is, even with the additional data herein presented, imperfectly known. The dots on the accompanying map (Fig. 1) represent localities in which I have studied arborescent or near-arborescent specimens (senescent, climax, or intermediate forms) of *S. louisiana* as well as the group discovered in Texas by Mr. Vines. The solid triangles indicate localities where the "field or pasture type" of *S. louisiana* is predominant and where sufficient study of the individuals in the field and of the flowers and fruits in the laboratory leaves no question as to their identity. It is not possible to give, on such a small-scale map, an accurate picture of the density of the palmetto populations in the respective areas. A dot may represent a single tree or a group. Several dots indicate extensive continuous or discontinuous stands. A solid triangle in all cases represents a tract of palmettos. The cross-hatched triangles indicate localities (36, 37, 40, and 41) where palmettos have been observed that appear to be *S. louisiana* but require further investigation of their flowers and fruits. Similar plants also occur in an alluvial area west of Charleston, S. C., and in a few other places not shown on the map.

There are numerous other palmetto areas, both within and beyond the known range of Louisiana palmetto, in which it is difficult to distinguish between the acaulescent *S. minor* and juvenile or dwarfed forms of *S. louisiana*, especially specimens that do not come into flower or fruit. Although much field work has already been done throughout the purported range of *S. minor*, further observation and a somewhat different approach through morphological studies is necessary for a better understanding of these two species.[23]

[23] My interest in native palmettos began in the New Orleans area while I was a member of the faculty of Tulane University (until 1932). A survey of Louisiana and some neighboring regions was made from May to November, 1933. Thereafter additional surveys and rechecking of areas previously visited were carried out during vacation periods from Washington, D. C., either in June or November (the flowering and fruiting seasons of *S. louisiana*). Grateful acknowledgment is made to former students and coworkers at Tulane University, especially Anna L. Haas, who accompanied me on many field trips and rendered assistance in the collection of material, measurement of specimens, and pH determinations of soil samples; to Mrs. J. R. Fowler, Dr. Mike Wright, and Dr. John W. Bick for help on various expeditions; and to Dr. Harley N. Gould and Dr. W. T. Penfound for extending the facilities of their respective laboratories to me subsequent to 1932. I am also indebted to G. D. Cain, County Agricultural Extension Agent, for information in connection with the palmettos of Richland Parish (Louisiana) and neighboring cotton-growing regions; Eloise R. Bomhard, who accompanied me on several surveys; E. L. Demmon, director of the Southern Forest Experiment Station (New Orleans), as well as a number of present and former Station staff members for numerous courtesies and assistance; Dr. B. C. Tharp, University of Texas, for cooperation and aid on field trips near Austin; and to various persons, who made prompt and helpful replies to my inquiries, especially Eula Whitehouse, Texas Memorial Museum.

The kind cooperation of Mr. Vines and Dr. Longley has already been mentioned. Thanks are also due Percy Viosca, Jr., of New Orleans, W. A. Dayton, U. S. Forest Service, and Dr. Penfound for reviewing the manuscript.

BOTANY.—*Two new basidiomycetous fungi parasitic on nematodes.*[1] CHARLES DRECHSLER, Bureau of Plant Industry.

Among several fungi set forth in an earlier paper (4) as attacking nematodes after the usual manner of parasites, by intrusion of hyphal elements arising through germination of adhering conidia, were included two species which from their production of clamp-connections were obviously to be reckoned among the Basidiomycetes. The two species, it was clear, were intimately akin to one another; yet owing to somewhat incidental differences in the make-up of their sporulating apparatus they could not both be assigned satisfactorily to any one mucedinaceous genus then available. Accordingly a new genus, *Nematoctonus*, was erected in which they were described under the names *N. tylosporus* and *N. leiosporus*. Subsequently two other forms, similarly parasitic on free-living nematodes, and similarly provided with clamp-connections, have been observed in transparent Petri-plate cultures. These two forms, which like those presented earlier have more than ordinary interest, since they represent basidiomycetes habitually subsisting on animals that normally remain in a motile state from the time of hatching until the approach of death, are described herein as additional species of *Nematoctonus*.

One of the two species came to light on September 1, 1942, in a maize-meal-agar plate culture that on August 24, 1942, had been planted with the softened stem of a newly damped-off tomato seedling from a greenhouse at the Bureau of Plant Industry Station near Beltsville, Md. The fungus, when first observed, was barely visible to the naked eye as a very delicate arachnoid weft festooned over a portion of the decaying tomato material. It failed to spread to other areas of the original culture, apparently for the reason that in its initial development all individuals of the susceptible species of nematode had been exterminated. However, when a small quantity of the delicate weft was transferred to another Petri-plate culture, which likewise had been started on August 24, from a damped-off tomato seedling, and which likewise had afforded ample development of free-living eelworms soon after the agar substratum became permeated with mycelium of *Pythium irregulare* Meurs, the arachnoid fungus resumed its destructive activity on a larger scale. Everywhere in the second culture it parasitized a single nematode species that manifestly was identical with the species it had exterminated in the original culture. The eelworm in question was determined by Dr. G. Steiner to belong to a group of forms that have been cited in the literature rather indiscriminately under the binomial *Rhabditis monhystera* Bütschli.

During the earlier stages of invasion the assimilative mycelium within an infected nematode is usually obscured very badly by the globulose materials resulting directly from degeneration of the host tissues. Later, when these globulose materials have in large part been appropriated by the fungus and have been utilized for the production externally of conidiophorous filaments (Fig. 1, *A*, *a*, *b*), the assimilative hyphae are better discernible. In some instances the empty membrane of the conidium (Fig. 1, *A*, *c*) that initiated the attack may then still be seen attached to the outside of the host integument, its prolongation in the empty germ hypha visibly communicating with the mycelium inside. Occasionally the empty envelopes of several conidia operative in accomplishing infection may be seen attached to the dead animal. The quantity of assimilative mycelium, however, would seem little influenced by the number of adhering spore envelopes, for multiple hyphae are readily produced by branching. Frequently branches arise directly from, or in close proximity to, clamp-connections, though some clamps having no special positional relationship to branches are usually present. Occurrence of clamps without relationship to branches or to any other lateral outgrowths could be noted also in external hyphae that happened to lie submerged for considerable distances under the surface of

[1] Received March 24, 1943.

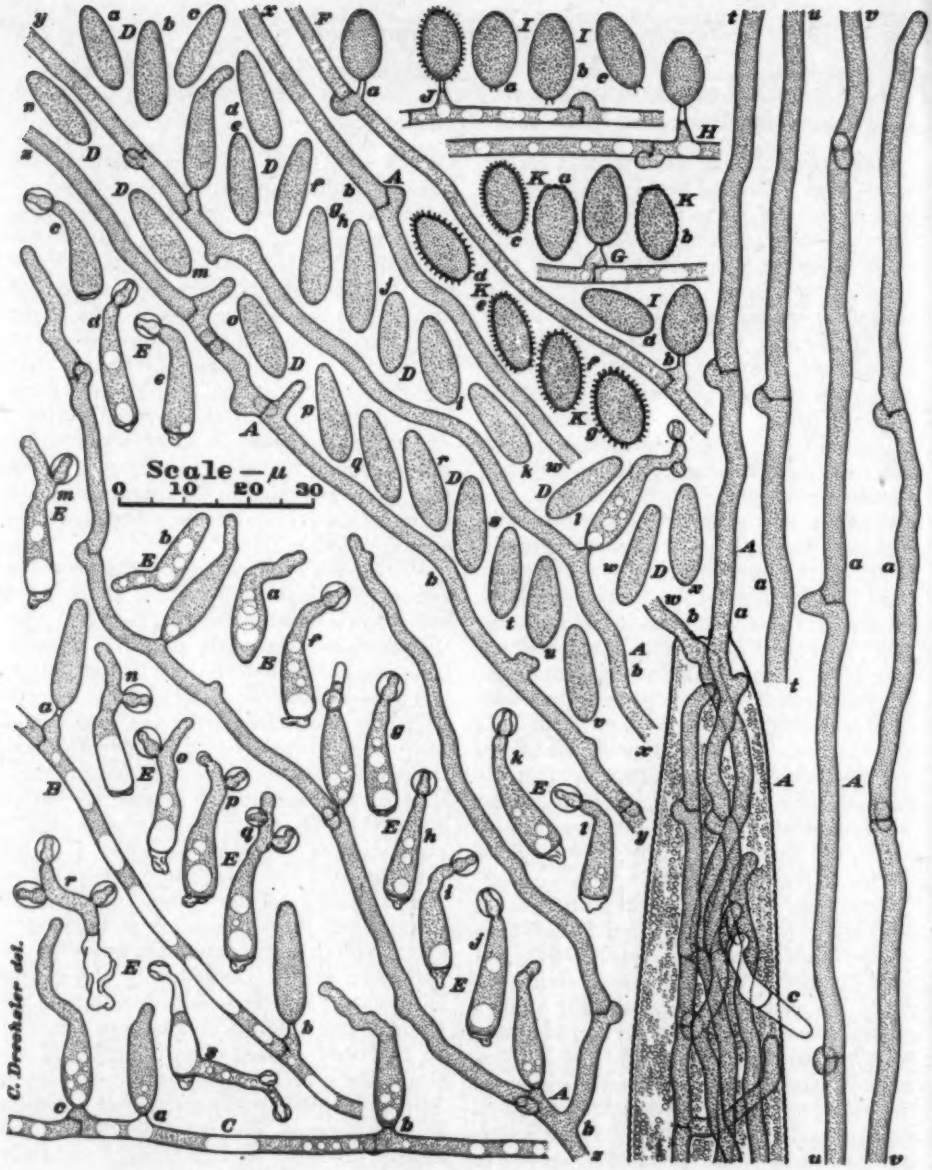

Fig. 1.—*Nematoctonus pachysporus*, drawn to a uniform magnification with the aid of a camera lucida; ×1,000 throughout. *A*, Anterior portion of nematode host permeated with assimilative mycelium from which one hypha, *a*, has been extended into the surrounding agar culture medium, while another hypha, *b*, has been extended into the air; the two external hyphae, from want of space, being shown in sections whose proper continuity is indicated by the two sequences of paired letters, *t*–*v* and *w*–*z*, respectively; *c*, empty envelope of conidium, attached externally, from which the assimilative mycelium had its origin. *B*, Portion of conidiophorous hypha, bearing conidia on two longish sterigmata, *a* and *b*. *C*, Portion of conidiophorous hypha bearing solitary conidia on three short sterigmata, *a*-*c*. *D*, Conidia, *a*-*x*, showing variations in size and shape previous to germinative development. *E*, Conidia, *a*-*s*, showing variations in germinative development. *F*, Portion of conidiophorous hypha with two sterigmata, *a* and *b*, whereon are borne solitary ovoid spores destined for conversion into resting spores. *G*, *H*, Portions of conidiophorous hypha, each with an ovoid spore soon to be converted into a resting spore. *I*, Three ovoid spores before conversion into resting spores. *J*, Portion of conidiophorous hypha showing an echinulate resting spore borne on a sterigma. *K*, Resting spores, *a*-*g*, showing variations in size, shape, and echinulation.

the agar culture medium (Fig. 1, *A*, *a*).

A submerged position, of course, is not a usual one for the external, conidiophorous filaments. Most often they grow out somewhat ascendingly into the air to attain lengths ranging from 1 to 1.5 mm. As their development continues they sooner or later decline to the substratum, so that eventually they come to lie prostrate in areas where the surface is smooth, or are draped loosely over prominences in more rugged areas. Occasionally a conidiophorous filament may grow out in a procumbent posture.

Whatever their posture may be, the aerial filaments become studded at intervals with clamp-connections, which often give rise, on short narrow sterigmata, to erect strobiliform conidia (Fig. 1, *A*, *b*; *B*, *a*, *b*). Conidia may, however, arise without any close positional relationship to clamp-connections (Fig. 1, *C*, *a*). Sometimes a conidium is borne almost sessile on the parent filament in close proximity to a clamp-connection (Fig. 1, *C*, *b*); or, again, it is attached, without any noticeable sterigma, directly to the dorsal side of a clamp (Fig. 1, *C*, *c*). Ordinarily its original strobiliform shape (Fig. 1, *D*, *a–x*) is soon modified as the result of germinative development. A short broad process is extended usually from the distal end (Fig. 1, *E*, *a*) or, in rare instances, from the basal end (Fig. 1, *E*, *b*). This process gives rise at its tip to a globose adhesive body, measuring usually 3 or 4μ in diameter, and consisting apparently of a narrowed hyphal termination together with a layer of glutinous secretion (Fig. 1, *E*, *c–l*). Thereupon the outgrowth may resume elongation (Fig. 1, *E*, *m–o*) to produce terminally a second adhesive body (Fig. 1, *E*, *p*, *q*). Elongation may then be resumed again, with eventual development of a third adhesive body (Fig. 1, *E*, *r*). In some instances where a germ outgrowth is put forth from the basal end as well as from the distal end, one of the outgrowths may form a single adhesive body while the other may produce two such bodies (Fig. 1, *E*, *s*). The transfer of protoplasmic materials required for such incipient germinative development is accompanied by vacuolization and evacuation usually of the basal portion of the conidium, and by collapse of the emptied portion of conidial envelope. Occasionally the entire protosplasmic contents may migrate into the stout germ outgrowth (Fig. 1, *E*, *r*).

In addition to the colorless thin-walled conidia discussed so far, the fungus produces resting spores. These likewise are mostly borne on short sterigmata arising from clamp-connections or in close proximity to clamp-connections (Fig. 1, *F*, *a*, *b*; *G*; *H*). During their earlier stages of development they resemble conidia, though usually they may be distinguished even then by their broader ovoid shape (Fig. 1, *I*, *a–d*). In their ripe condition (Fig. 1, *J*) they have a perceptibly yellowish coloration, and individually are surrounded by a thicker wall, which sometimes is modified externally with bullate sculpturing (Fig. 1, *K*, *a*, *b*), but oftener is closely beset with slender spiny protuberances (Fig. 1, *K*, *c–g*). As these resting spores have never been seen to germinate, it may be presumed that like the resting spores of *Nematoctonus tylosporus* they are adapted for tiding over unfavorable periods.

The greater thickness of its conidia relative to the conidia of the three known congeneric species suggests the epithet proposed for the fungus.

Nematoctonus pachysporus, sp. nov.

Hyphae assumentes incoloratae, irregulariter ramosae, plerumque 2–3.5μ crassae, in modum Hymenomycetum septato-nodosae, intra vermiculum nematoideum viventem crescentes, post mortem animalis aliquot hyphas fertiles extra emittentes; hyphis fertilibus incoloratis, simplicibus vel parce ramosis, primo plerumque ascendentibus postea procumbentibus, mediocriter septato-nodosis, vulgo 0.5–1.5 mm longis, 2.2–3.2μ crassis, conidia vel sporas perdurantes quandoque protinus ex nodis quandoque ex sterigmatis singulatim gerentibus; sterigmatis erectis, 0.5–5μ longis, basi 1–2.5μ crassis, apice 0.6–1μ crassis; conidiis incoloratis, primo continuis et erectis, levibus, elongato-ellipsoideis vel strobiliformibus, plerumque 12–19μ longis, 4–5.5μ crassis, ex apice vel rarius ex basi hypham germinationis brevem erectam emittentibus; hac hypha 1–3 corpora glutinosa 2.5–5.5μ crassa deinceps proferente. Sporae perdurantes continuae, ovoideae, flavidae, verrucosae

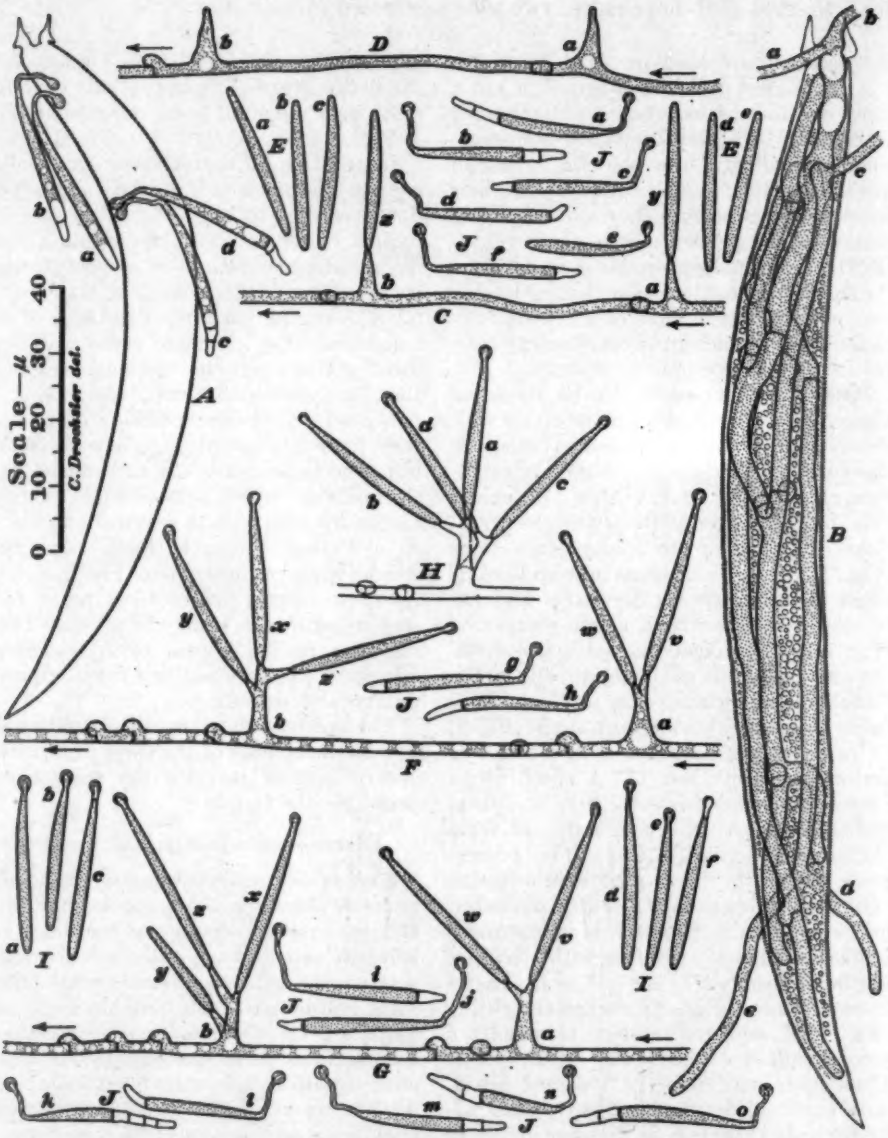

Fig. 2.—*Nematoctonus leptosporus*, drawn to a uniform magnification with the aid of a camera lucida; ×1,000 throughout. *A*, Young specimen of *Bunonema* sp. to which are attached four germinating conidia whose vacuolate condition indicates that each may be extending an infective hypha into the animal. *B*, Nematode host permeated with a mycelium from which five hyphae, *a-e*, have begun to grow externally. *C*, Portion of conidiophorous hypha with two sterigmata, *a* and *b*, each bearing a single conidium that shows no apical adhesive modification. *D*, Portion of conidiophorous hypha with two denuded sterigmata, *a* and *b*. *E*, Detached conidia, *a-e*, showing variations in size and shape before undergoing apical modification. *F*, *G*, Portions of conidiophorous hypha, each with two branching sterigmata, one of them, *a*, bearing two spores, *v* and *w*, while the other, *b*, supports three spores, *y-z*. *H*, Portion of conidiophorous hypha with a branched sterigma bearing four conidia, *a-d*, all modified at the apex. *I*, Conidia, *a-f*, each of which formed an adhesive knob at its apex before becoming detached from its sterigma. *J*, Conidia, *a-o*, that after falling on moist agar culture medium have each sent up a delicate apical process terminating in a small adhesive knob.

vel crebre echinulatae, 10–13μ longae, 5.5–7.5μ crassae.

Vermiculum nematoideum Rhabditis monhysterae adfinem enecans habitat in radicibus Lycopersici esculenti putrescentibus prope Beltsville, Maryland.

Assimilative hyphae colorless, irregularly branched, mostly 2 to 3.5μ wide, provided with clamp-connections, developing within living nematodes, after death of host animal giving rise externally to several conidiophorous hyphae. Conidiophorous hyphae colorless, simple or somewhat branched, at first usually ascending, later prostrate or festooned on the substratum, commonly 0.5 to 1.5 mm. long, 2.2 to 3.2μ wide, at moderate intervals (mostly 10 to 75μ) forming clamp-connections, producing solitary conidia or solitary resting spores sometimes directly on clamp-connections and at other times on sterigmata 0.5 to 5μ long, 1 to 2.5μ wide at the base, 0.6 to 1μ wide at the apex. Conidia erect, colorless, smooth, at first continuous, elongate-ellipsoid or strobiliform, mostly 12 to 19μ long, 4 to 5.5μ wide, before or after disjunction usually becoming partly evacuated of contents in giving rise at the apex or more rarely at the base to a short erect process whereon are borne successively 1 to 3 globose adhesive bodies 2.5 to 5.5μ in diameter. Resting spores aseptate, yellowish, ovoid, at maturity warty or strongly echinulate, measuring mostly 10 to 13μ in length and 5.5 to 7.5 μ in width.

Destroying a species of nematode belonging to the *Rhabditis monhystera* group, it occurs in decaying roots of *Lycopersicon esculentum* near Beltsville, Md.

The other species of *Nematoctonus* to be presented herein was found developing abundantly in Petri plates of maizemeal agar, which after being permeated with *Pythium* mycelium had been further planted with pinches of friable leaf mold taken from deciduous woods near Fairfax, Va., on November 10, 1942. In these cultures it subsisted exclusively on a species of *Bunonema* introduced with the forest refuse. Invasion of the small eelworm was manifestly initiated by continued germinative development of adhering conidia (Fig. 2, *A*, *a–d*), though owing to optical difficulties arising from globulose degeneration of the host tissues, not to mention further difficulties attributable to pronounced sculpturing of the host integument, the progress of mycelial advance could not be followed. However, after the granular materials had been largely appropriated the assimilative mycelium was revealed, though often only rather indistinctly, as a branching system of hyphae studded here and there with clamp-connections (Fig. 2, *B*). Usually before this somewhat transparent condition came about, conidiophorous filaments were being extended over the surface of the adjacent substratum (Fig. 2, *B*, *a–e*).

These filaments, while still elongating, give rise at moderate intervals to erect tapering sterigmata (Fig. 2, *C*, *a*, *b*; *D*, *a*, *b*), each bearing at its tip a slender, slightly tapering, rod-shaped conidium (Fig. 2, *C*, *y*, *z*) whose apex in the beginning shows no special modification (Fig. 2, *E*, *a–e*). Sometimes a sterigma grows directly from a clamp-connection but more often it arises some little distance backward from a clamp, that is, some little distance nearer the origin of the filament (Fig. 2, *C*, *a*, *b*; *D*, *a*, *b*). After the individual sterigma (Fig. 2, *F*, *a*; *G*, *a*) has produced its first conidium (Fig. 2, *F*, *v*; *G*, *v*), it ordinarily continues in its reproductive function by putting forth a short lateral spur on which a second conidium is formed (Fig. 2, *F*, *w*; *G*, *w*). Many sterigmata thereupon will put forth a second lateral spur, and thus will come to support three conidia (Fig. 2, *F*, *x–z*; *G*, *x–z*). In mature portions of conidiophorous hyphae some sterigmata can be found bearing as many as four conidia, each, of course, borne on a separate sterigmatic tip (Fig. 2, *H*, *a–d*).

Branched sterigmata bearing two or three conidia are nearly always to be found in proximity to a corresponding number of clamp-connections (Fig. 2, *F*, *G*). Apparently the clamps of later origin are formed in successively more distal positions.

Soon after they have been cut off by a basal septum, the conidia undergo noticeable germinative development. Those that remain supported on their sterigmata produce at the tip a globose knob consisting of a glandular part thinly surrounded with adhesive secretion (Fig. 2, *F–H*; *I*, *a–f*). Those that become detached and fall on a

moist surface produce a similar adhesive knob terminally on a delicate, erect or ascending process extended from the tip (Fig. 2, *J*, *a–o*). The materials required for this germinative development are supplied through evacuation of protoplasm from the basal portion of the conidium. To separate the living portion of the spore from the emptied portion at least one retaining wall is laid down. In instances where presumably the movement of protoplasm takes place rather slowly, two (Fig. 2, *J*, *a*, *b*, *m*, *n*, *o*) or even four (Fig. 2, *J*, *k*) retaining walls may be laid down successively.

Comparable development of adhesive knobs on delicate processes arising from fallen conidia has not been noted in *Nematoctonus tylosporus*. The fungus differs further from *N. tylosporus* in its markedly stronger tendency toward production of conidia plurally on branching sterigmata. Its conidia, moreover, are appreciably narrower and longer than those of *N. tylosporus*, and, of course, pronouncedly narrower and longer than the conidia of *N. leiosporus* and *N. pachysporus*. A term having reference to its slender spores may therefore serve as an epithet sufficiently descriptive to set the fungus apart from the three known congeneric forms.

Nematoctonus leptosporus, sp. nov.

Hyphae assumentes incoloratae, plus minusve ramosae, plerumque 2–3.5μ crassae, in modum Hymenomycetum septato-nodosae, intra vermiculum nematoideum viventem crescentes, post mortem animalis aliquot fertiles hyphas extra emittentes; hyphis fertilibus incoloratis, saepius procumbentibus, modice septato-nodosis, vulgo 250–750μ longis, 1.6–2μ crassis, conidia ex erectis sterigmatis gerentibus; his sterigmatis inter se saepius 35–65μ distantibus, 5–10μ altis, basi 2.5–4μ crassis, sursum attenuatis, apice .5–1μ crassis, primo simplicibus, postea 1–3 ramusculos emittentibus, itaque vulgo 2 vel 3 etiam quandoque 4 conidia proferentibus; conidiis incoloratis, bacillaribus, sursum leviter attenuatis, utrinque obtusulis vel rotundatis, 21–28μ longis, 1.7–2.2μ crassis, primo continuis et protoplasmatis omnino repletis, mox in parte infera vacuis et apice tuberculo glutinoso circa 2μ crasso praeditis, postea tuberculum ejusmodi in apice hyphae erectae vel ascendentis 3–10μ longae .6μ crassae ferentibus.

Vermiculum nematoideum speciei Bunonematis necans habitat in humo silvestri prope Fairfax, Virginia.

Assimilative hyphae colorless, provided with clamp-connections, somewhat branched, mostly 2 to 3.5μ wide, developing within living nematodes, after death of host animal producing several conidiophorous hyphae externally; conidiophorous hyphae colorless, usually prostrate, commonly 250 to 750μ long, 1.6 to 2μ wide, forming clamp-connections at moderate intervals, giving rise to conidia on erect sterigmata; the sterigmata spaced mostly at intervals of 35 to 65μ, at first simple, commonly 5 to 10μ high, 2.5 to 4μ wide at the base, tapering upward, mostly 0.5 to 1μ wide at the tip, later usually putting forth 1 to 3 lateral spurs and by producing a conidium on each spur eventually coming to support 2 or 3 or sometimes even 4 conidia; the conidia colorless, staff-shaped, tapering slightly toward apex, somewhat obtuse or bluntly rounded at both ends, mostly 21 to 28μ long and 1.7 to 2.2μ wide, at first continuous, later often empty at the base and provided at the tip with a globose adhesive knob about 2μ wide, or after falling off producing such a knob terminally on an erect or ascending process, 3 to 10μ long and 0.6μ wide, that is extended obliquely or perpendicularly from the tip.

Parasitic on a species of *Bunonema* in leaf mold near Fairfax, Va.

With respect to outward shape the knob-bearing outgrowth commonly produced by the conidium of *Nematoctonus leptosporus* after falling on a moist surface offers curious similarity to the empty basal appendage on the conidium of *Euryancale sacciospora* Drechsl. (3) as well as to the proximal portion of the conidium of *Harposporium oxycoracum* Drechsl. (4). This similarity would seem in large measure illustrative of convergence, since the three fungi, remote from one another taxonomically, all subsist as obligate parasites on nematodes of the genus *Bunonema*. The adaptive modifications here concerned may well have been developed to facilitate attachment of the conidia to the strongly sculptured integument so characteristic of the host animals in their adult condition.

In *Nematoctonus pachysporus* the development of adhesive bodies plurally, together with the frequently pronounced exhaustion of the spore, makes for an appearance not wholly unlike that offered in the development of basidiospores on basidia. The homologies thus suggested can not readily be dismissed until adverse cytological evidence has been brought foreward, or until structures have been discovered more closely corresponding to basidia than any I have observed hitherto. The plural adhesive bodies, it is true, are almost certainly of the same character as the single adhesive knobs formed in the three congeneric species; but the possibility remains that these single knobs, however commonplace their appearance, might yet represent abortive basidiospores modified for adhesion. Nevertheless, the thin-walled aerial spores still seem best interpretable as conidia, especially since in their manner of formation they offer strong parallelism with the binucleate conidia described by Nobles (5) as being produced on clamp-bearing mycelia of *Corticium incrustans* Höhn. & Litsch. If the four parasitic species so far described all produce typically straight conidia, the Hawaiian nematode-capturing fungus to which reference was made earlier (4, p. 780) and which almost certainly is intimately related to the parasitic species, produces conidia that resemble those of *C. incrustans* in being of curved allantoid shape.

Their constant production of clamps rather definitely removes all five of the fungi habitually subsisting on eelworms from close kinship with *Septobasidium* Pat., a large genus of basidiomycetes whose parasitism on scale insects, affirmed by Reinking (6) in 1919, has more recently been set forth in detail by Couch (2). On similar grounds they must be considered taxonomically remote from *Uredinella* Couch, likewise a genus of basidiomycetes parasitic on scale insects, since at least in *U. coccidiophaga* Couch (1), just as in all species of *Septobasidium*, clamp-connections are absent.

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ORNITHOLOGY.—*A new race of the sharp-tailed grouse.*[1] HERBERT FRIEDMANN, U. S. National Museum.

Snyder's papers on the sharp-tailed grouse,[2] in spite of certain faults, may be said to have furthered our knowledge of this bird more than any that went before. A recent study of this species, based on over 200 specimens, indicates, however, that parts of Snyder's arrangement of races needs alteration. These changes, herein proposed, have to do, firstly, with the birds of the far Northwest, which he calls *kennicottii*, and secondly with the ranges of *jamesi* (which includes the *campestris* of Snyder's first two papers) and of *campestris* (with which Snyder's *campisylvicola* is synonymized).

To take the northwest Canadian and the Alaskan birds first, we find that a series of topotypical *kennicottii* from Fort Rae and Fort Simpson, differ markedly from a long series (40 specimens) from Alaska southeastward to Tagish Lake on the Yukon-British Columbia border and to extreme Northern Alberta. Inasmuch as there seems to be no name available for the Alaskan birds, it is proposed to call them—

[1] Published by permission of the Secretary of the Smithsonian Institution. Received April 3, 1943.

[2] SNYDER, L. L., *A study of the sharp-tailed grouse.* Univ. Toronto Stud., Biol. Ser., **40** (2). 1935; *A revision of the sharp-tailed grouse with a description of a new race.* Occ. Pap. Roy. Ontario Mus. Zool., no. 2. 1935; *Great Plains races of the sharp-tailed grouse.* Auk **56**: 184–185. 1939.

Pedioecetes phasianellus caurus, n. subsp.

Type.—U.S.N.M. 298189. ad. ♂, collected at Fairbanks, Alaska, October 19, 1921, by O. J. Murie.

Subspecific characters.—Differs from *kennicottii* in having the feathers of the upperparts much more broadly and abundantly barred with brown and, on the mantle, with white, and with the white spots larger, the feathers of the breast white, edged with dark olive-brown (instead of dark buffy brown with only a narrow white shaft stripe); from *jamesi* (as understood in this paper—the bird of the Great Plains from central Alberta to northeastern Colorado) this form differs in being much darker, more black showing above, the brown barrings darker, and the edgings of the breast feathers darker; from *columbianus* it differs in being darker and larger.

Description of type.—Forehead fuscous to fuscous-black, the feathers tipped with dark snuff brown; feathers of the crown and occiput similar but crossed with widely spaced whitish bars and tipped with cinnamon-buff; the pale bars more abundant, less widely spaced on the lateral coronal feathers, and blending into a fairly definite whitish or buffy whitish superciliary stripe on each side; nape like the sides of the crown but washed with pale ochraceous-buff; "mantle," i.e., interscapulars, fuscous-black broadly barred with white, the more distal bars, especially on the more posterior feathers, washed with pale ochraceous-buff; feathers of sides of neck and of breast similar to anterior interscapulars; back, rump, and upper tail coverts fuscous-black, broadly but incompletely barred with cinnamon-buff to tawny-olive, the latter color often sparsely vermiculated with fuscous-black and broadly tipped with pale cinnamon-buff to pinkish buff, darkest on the back and becoming paler on the rump and upper tail coverts; scapulars and inner median and greater upper wing coverts like the upper back but with the brownish areas more extensive (at the expense of the blackish parts) and each feather with a large terminal white wedge-shaped spot; rest of the upper wing coverts and the secondaries grayish olive-brown externally incompletely and sparsely barred with white, the coverts with terminal white spots on their outer webs, the secondaries completely edged with white on the tips of both webs; primaries grayish olive-brown with white spots on the outer webs; median rectrices pinkish buff longitudinally and transversely marbled with fuscous-black; the next pair largely fuscous-black tipped with white and with their outer webs mixed with white; lateral rectrices white with dusky smudges along the shafts; circumocular region fuscous-black; lores, subocular stripe, cheeks, and auriculars pale ochraceous-buff dappled with dusky, the dusky markings concentrating on each side to form a fairly distinct malar stripe; the auriculars tipped with fuscous-black; chin and upper throat whitish suffused with pale ochraceous-buff and with many small pale clove-brown spots; lower throat white, the feathers narrowly edged with dark olive-brown; breast feathers white with heavy margins of dark olive-brown; feathers of sides and flanks white barred with dark olive-brown, the more posterior of these feathers with considerable tawny-olive on their outer webs and with the dark bars darker—clove-brown to almost fuscous; upper abdomen and sides of lower abdomen white with a few small dark olive-brown subterminal V-shaped marks; center of abdomen and under tail coverts white, sometimes tinged with pale ashy buff; thighs pale light cinnamon-drab, the distal tarsal plumes paler, more whitish and very long, covering all but the claw of the middle toe.

Females in comparable (autumn and winter) plumage are like the male but their median rectrices are more strictly transversely barred, less longitudinally marbled with blackish than are those of the male.

Measurements of type.—Wing 207; tail 114; culmen from anterior end of nostril 11.8; tarsus 43; middle toe without claw 38.2 mm.

Thirteen adult males measure as follows: wing 196–212 (203.2); tail 113–125 (118.7); culmen from anterior end of nostril 10.3–11.8 (10.9); tarsus 40.4–44.3 (42.3); middle toe without claw 36–39.2 (38.1); height of bill at base 10.3–12.4 (11.5 mm).

Thirty-three adult females measure: wing 190–202 (196.3); tail 107–119 (111.9); culmen from anterior end of nostril 9.9–11.9 (10.8); tarsus 39.2–42.8 (41.2); middle toe without claw 35.7–39.3 (37.5); height of bill at base 10.9–12.5 (11.8 mm).

Range.—This form occurs from north-central Alaska (Circle, Fairbanks, Tanana, Tanana Crossing, north Fork Kuskokwim River, Delta

and Taklat Rivers) to the southern Yukon Province (Tagish Lake on the Yukon-British Columbia border) and to extreme northeastern Alberta (Fort Chipewyan, Smith Landing, Fort Smith, Peace Point).

The separation of this new form leaves *P. p. kennicotti* with a much restricted range, occupying merely northern Mackenzie (Fort Rae to Fort Simpson). This form is very distinct from *caurus;* in fact it is nearer to, but easily told from, typical *phasianellus* of the Hudson Bay region.

Turning now to the birds of the Great Plains and the Prairies, we find, if we take birds in fresh autumn plumage, that specimens from the Prairies (Illinois, Wisconsin, Minnesota, and southern Manitoba) are more rufescent (ochraceous-tawny to almost hazel) on the upper parts, while birds from the Great Plains (north-central Alberta, central Saskatchewan, most of Montana, the Dakotas, Wyoming, western Nebraska, and northeastern Colorado) have the upperparts buckthorn brown or grayer. The prairie birds are obviously *P. p. campestris* (type locality—Illinois), while for the less rufescent birds of the Plains the name *jamesi* (type locality—Castle Rock, Colo.) is available. In the latter race there is a slight paling in the southern part of the range, but on the whole it seems ill-advised to attempt to separate Alberta birds from specimens from Wyoming and Colorado. Northern *jamesi* shows an approach toward *caurus*. Good series of both *jamesi* (86 adults) and of *campestris* (18 adults) have been examined in this connection. The characters on which *jamesi* was originally proposed do not seem to mean much, but the name is nevertheless applicable to the group as here defined. It is the most variable of all the races of the sharp-tailed grouse.

The ranges of typical *phasianellus* and of *columbianus* are essentially correctly given by Snyder, but the range of the latter should be extended to the Modoc region, northern California.

KEY TO THE FORMS OF PEDIOECETES PHASIANELLUS

a. Darker above, the black or dark fuscous areas predominating, giving an appearance of a dark bird barred with buffy brown and spotted with white.

b. Upperparts very dark, the brownish barrings and edges and tips of the feathers of the mantle and upper back much reduced, the marks in the inner portions of the vanes very narrow or absent; feathers of the breast dark buffy brown with only narrow white shaft stripes (central and northern Mackenzie)..... *Pedioecetes phasianellus kennicottii* Suckley

bb. Upperparts less dark, the brownish barrings and edges and tips of the feathers well developed.

c. White spots on the upper parts much reduced; feathers of breast pale buffy brown with fairly broad white shaft stripes (Hudson Bay region).. *Pedioecetes phasianellus phasianellus* (Linnaeus)

cc. White spots on the upper parts large and prominent; feathers of breast white, merely edged with dark olive-brown (Alaska, the Yukon District to extreme northern British Columbia)..... *Pedioecetes phasianellus caurus*, n. subsp.

aa. Paler above, the brown areas larger, the blackish ones more hidden, giving the appearance of a brownish bird mottled with blackish.

b. Brown of upperparts more rufescent—ochraceous-tawny to almost hazel (Illinois, Wisconsin, Minnesota, and southern Manitoba)..... *Pedioecetes phasianellus campestris* Ridgway

bb. Brown of upperparts less rufescent—buckthorn brown to tawny-olive.

c. Smaller and paler; tail averaging less than 110 mm; height of bill at base averaging 12 mm; brown of upperparts tawny-olive (from north-central British Columbia to northern California (Modoc region), Nevada, Utah, and southwestern Colorado)..... *Pedioecetes phasianellus columbianus* (Ord)

cc. Larger and darker; brown of upperparts buckthorn brown; tail averaging over 115 mm; height of bill at base averaging 13 mm (Great Plains and from north-central Alberta, central Saskatchewan, to (all but extreme western) Montana, the Dakotas, Wyoming, western Nebraska, and northeastern Colorado)... *Pedioecetes phasianellus jamesi* Lincoln

Obituary

HARRY JOHN MCNICHOLAS was born in Plymouth, Wis., on October 29, 1892, and died in Washington, D.C., on July 23, 1942, of heart failure.

Mr. McNicholas graduated from the Plymouth High School in 1910, entered Ripon College in 1911, and "worked his way" to the A.B. degree in 1915. During his last two years in college he defrayed his expenses by acting as assistant mail carrier. For diversion he played a trumpet in the Ripon College Band. This is mentioned because it played a part in shaping his subsequent career. The writer, having previously played a trombone in this band, joined the staff of the Bureau of Standards in 1914, and for amusement organized a small orchestra, but no trumpet player could be found on the staff. In 1915 we wrote to Professor Barber at Ripon College suggesting that the pending Civil Service examination be called to the attention of his best physics student, especially if he played a trumpet. Mr. McNicholas took this examination and promptly accepted an appointment as laboratory assistant in the Colorimetry Section, where he worked on color standardization until 1926. He was then transferred to the Textile Section to initiate researches on the physical structure of cellulose and rubber, including Röntgen-ray analysis. When depression curtailed this work in 1933, Mr. McNicholas was detailed for a year to investigate optical properties of glass and other materials used in identification lights on airplanes, then appointed to work on the utilization of wasteland products, and finally on pH standards in the Chemistry Division. In February 1941 he was engaged in defense work on methods of establishing acidity of lubricating and transformer oils and gasolines. His ability, industry, and scientific work were rewarded by successive promotions from laboratory assistant to full physicist.

Being studious by nature, Mr. McNicholas enrolled for many graduate courses in physics and mathematics given at the Bureau of Standards from 1915 to 1937. In 1924 he received an M.A. degree and in 1926 a Ph.D., both from the Johns Hopkins University. Unlike the men who think their formal education is completed when the Ph.D. is awarded, Dr. McNicholas continued to attend classes for specialized study of such topics as the interpretation of data, probability and statistics, and chemical thermodynamics.

His name appears on a score of scientific papers published since 1919. In a series of important papers of which he was sole author he demonstrated that he had exceptional talents for instrument design, for analysis of scientific observations, and for lucid literary exposition. The following, published as research papers in the Journal of Research of the National Bureau of Standards, deserve special mention: Absolute methods in reflectometry (RP3), Equipment for routine spectral transmission and reflection measurements (RP30). The visible and ultraviolet absorption spectra of carotin and xanthophyll and the changes accompanying oxidation (RP337), Equipment for measuring the reflective and transmissive properties of diffusing media (RP704), Color and spectral transmittance of vegetable oils (RP815), and Selection of colors for signal lights (RP956).

Dr. McNicholas possessed a quiet, modest, and unassuming but genial disposition, and he had a large number of friends who always called him by his nickname, "Pat." After many years of sedentary life in crowded apartments he purchased a home and yard and took great pleasure in landscaping and gardening activities, which he liked to begin at daybreak.

In 1916 he married Gertrude M. Weingarten of Ripon, Wis. He is survived by his mother and four sisters, his wife and daughter, Mrs. Kathlyn Fitzgerald, and four grandchildren.

WILLIAM F. MEGGERS